Environmental Influences on Annual Migrations of Juvenile Southern Bluefin Tuna (*Thunnus maccoyii*)

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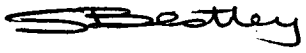
Fieldwork collecting otoliths from juvenile SBT in Esperance WA, January, 2004.
(Photograph: Thor Carter)

Statement Of Originality

This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis. To the best of my knowledge and belief, this thesis contains no material previously published or written by another person except where due acknowledgement is made in the text of the thesis.



27/11/08

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Statement of Authority of Access

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Sophie Bestley Date

Dedication

To my mother Susan Capilli for always encouraging us to do what brings us joy

Abstract

Understanding the movement of animals in time and space, and its implications for the abundance and distribution of populations, is a pivotal problem in ecology. Animal migration is often interpreted as a response to environmental heterogeneity, particularly in dynamic ocean environments where prey resources tend to be patchily distributed. In juvenile animals, since migration is not associated with travel to breeding sites, movement is expected to be more tightly coupled to food resources.

This study is concerned with the migratory patterns of the juvenile animals of a large, predatory, widely distributed temperate marine species, the southern bluefin tuna (*Thunnus maccoyii*, hereafter SBT). The long-distance migrations of this predator are investigated directly within the oceanographic context, with environmental influences on movement and behaviour determined through the integration, analysis and interpretation of telemetry-based and oceanographic data. In this thesis I present data and analyses for:

(1) *Seasonal ocean processes* – remotely sensed ocean data were used to identify oceanographic features, and their cycle of development and/or productivity, that may provide important seasonal feeding habitats.

(2) *Plasticity in vertical behaviour* – oceanographic habitats were characterised on the basis of water column structure, using temperature-at-depth data from archival tags, and vertical movements of SBT examined in response to habitat type and other factors.

(3) *Feeding and foraging ecology* – temporal feeding patterns were determined from visceral warming patterns and used to evaluate the relationship between feeding success and time spent in an area.

(4) *Factors predictive of feeding success* – were investigated using an integration of telemetry, environmental data and statistical modelling techniques.

General discussion – the integration of biological and oceanographic data provide a significant advancement to our current knowledge on movement, habitat use and

foraging ecology in migratory marine animals, and an increased appreciation for the diversity and complexity of biological phenomena. In particular, the ability to detect feeding events provided critical, and sometimes unexpected, insights into the motivations for the observed movements and behaviours, challenging some existing ecological concepts.

Statement of publication and co-authorship

Publications produced as part of this thesis:

Bestley S, Gunn JS, Marsac F (*in review*) Influence of seasonal ocean dynamics on the migrations of juvenile southern bluefin tuna. *Progress in Oceanography (1st CLIOTOP Symposium Special Issue).*

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Bestley S, Patterson TA, Hindell MA, Gunn JS (2008) Feeding ecology of wild migratory tunas revealed by archival tag records of visceral warming. *Journal of Animal Ecology*, 77, 1223-1333.

Bestley S, Patterson TA, Hindell MA, Gunn JS (*submitted*) Predictors of feeding success in a wild migratory fish: integrating telemetry, environmental data and modelling techniques. *Ecology.*

The following people and institutions contributed to the publication of the work undertaken as part of this thesis:

- *John S. Gunn (CSIRO Marine and Atmospheric Research) and Mark A. Hindell (University of Tasmania) assisted with guidance and supervision in all aspects of the PhD and producing publishable quality manuscripts*
- *Toby A. Patterson (CSIRO Marine and Atmospheric Research) provided assistance with usage of the feed event data and producing publishable quality manuscripts*
- *Francis Marsac (Insitut de Recherche pour le Developpement) provided assistance with the empirical orthogonal functions and producing publishable quality manuscripts*
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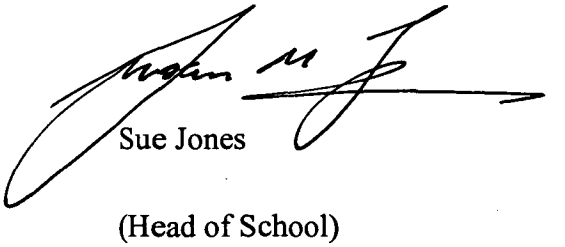
- *Katherine Tattersall (CSIRO Marine and Atmospheric Research) aided in the quality control of the archival tag data and the identification of all the feed events within the custom CSIRO software ARCHTAG©*
- *John S. Gunn, Naomi Clear, Thor Carter and Clive Stanley (all at CSIRO Marine and Atmospheric Research) undertook fieldwork for the deployment of tags during the austral summers of 1998–2000*

We the undersigned agree with the above stated "proportion of work undertaken" for each of the above published (or submitted) peer-reviewed manuscripts contributing to this thesis:

Mark Hindell

(Candidate's Supervisor)



Sue Jones

(Head of School)

Acknowledgements

In the beginning it all seems reasonable, and you convince yourself that this PhD will be smooth and co-ordinated, not subject to the wild erratic nature you've seen so many times before. In practice, candidates tend to be the same dedicated yet curiosity-driven creatures, and to steer us through the sometimes difficult journey we rely on the patience, generosity and guidance of many others.

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1. General Introduction

Understanding the movement of animals in time and space, and its significance for the abundance and distribution of populations, is a pivotal problem in ecology. Animal migration is often interpreted as an evolutionary and ecological response to environmental heterogeneity *i.e.* the spatial and/or temporal patchiness of resources in the environment. Perhaps the most famous instances are the massive seasonal overland migrations made by herd-dwelling mammals such as wildebeests (*Connochaetes taurinus*) and caribou (*Rangerifer tarandus*) (Berger 2004). A stunning example in a marine species is the inter-hemispheric migrations undertaken by sooty shearwaters (*Puffinus griseus*) between breeding and foraging grounds (Shaffer *et al.* 2006). Dynamic ocean environments in particular tend to have heterogeneous and patchily distributed resources (Mann & Lazier 2005). In juvenile animals, since migration is not associated with travel to breeding sites, movement is expected to be tightly coupled to food resources. This study is concerned with the migratory patterns of the juvenile animals of a large, predatory, widely distributed temperate marine species, the southern bluefin tuna (SBT), *Thunnus maccoyii*. The long-distance migrations of this pelagic predator are investigated directly within the oceanographic context, and environmental influences on movement and behaviour determined through the integration, analysis and interpretation of telemetry-based and oceanographic data.

MIGRATION STRATEGIES

Migration is a fundamental component of the life-history and ecological niche of many organisms (Dingle & Drake 2007). The phenomenon of animal migration was described by (Dingle 1996) as a persistent and directed movement of animals from one habitat to another. An even broader generalization, the act of moving from one spatial unit to another, was previously adopted by (Baker 1978) in an effort to avoid any restriction in the definition. Migration has evolved independently among many animal groups including birds, mammals, fish, reptiles, insects and invertebrates, and occurs by flying, swimming, walking/running or drifting on winds or currents. The diverse expression of

migration patterns covers orders of magnitude in spatial scales, from metres to trans-oceanic and including both horizontal and vertical planes of movement; and temporal scales of minutes to years. Common elements of migrations may include some form of return movement, or some degree of directedness, periodicity, and distance; however among animal movements, all components may show continuous variation between extremes (Baker 1978).

From the great flexibility displayed in the evolution of migratory patterns, it can be expected that to a large degree, migration evolved according to the ecological opportunities (Alerstam, Hedenstrom & Akesson 2003). For example, many fish migrations take place to locate suitable spawning areas, with particular abiotic (*e.g.* temperature, currents) and biotic (*e.g.* suitable food resources for developing larvae, reduced or absent predation threat) characteristics. Additional complexity occurs in migrations that are not for breeding/spawning and cannot be defined as a simple ontogenetic shift (Pittman & McAlpine 2003). In many cases, migration is an adaptation to resources, such as food, shelter and favourable climatic conditions, that fluctuate spatio-temporally, allowing peaks of resource abundance to be exploited and resource depression to be avoided. Particularly in unstable or unpredictable habitats there will be little or no benefit to continuous site fidelity, favouring the development of migrations (Alerstam & Enckell 1979). At a minimum, a habitat must enable survival, while better quality habitats will allow feeding, growth and development.

Long-distance terrestrial migrations are often spectacular (*e.g.* annual migrations of swallows or wildebeests), or of critical economic importance (*e.g.* plague locusts), and have long been followed by researchers. The advantage being (1) terrestrial animals are directly observable, and (2) so is their natural habitat. In contrast to terrestrial biology the characteristics of the marine environment, with the poor optical qualities of water and the added dimension of depth, have meant visual observation could provide evidence on only a fraction of the lives of fast, long-ranging and often long-lived animals such as marine mammals (*e.g.* pinnipeds, cetaceans), birds (*e.g.* penguins, albatross), reptiles (*e.g.* turtles) and fish (*e.g.* tunas, sharks). The movement patterns of these highly mobile species may be very complex, and the range of temporal and spatial scales involved can

present both a conceptual and operational problem for designing ecological studies (Pittman & McAlpine 2003). Animal-attached remote-sensing technologies (for reviews see Cooke *et al.* 2004; Ropert-Coudert & Wilson 2005), such as electronic data storage tags, therefore provided a critical development for research on large marine predators which migrate over or within oceans.

Migration is effected by individuals, the unit upon which natural selection acts, but the process has outcomes for both the individual and the population. A valuable approach to studying migrating animals, in terms of behavioural ecology, is therefore to examine the behaviour of the individual, within the context of their natural environment, and seek explanations in terms of the ecological function. Relative to other techniques, telemetry provides high spatial and temporal resolution data, across multiple habitats and at the scale appropriate to the animals behaviour. The 'organism-eye' perspective allows unprecedented insight into poorly understood linkages between the migratory paths of marine animals and environmental and oceanographic conditions. The outstanding questions of how animal movement, behaviour and foraging activity are shaped by environmental factors can begin to be addressed for highly migratory species in marine systems.

SOUTHERN BLUEFIN TUNA AS A MODEL SPECIES

Biology

Southern bluefin tuna (*Thunnus maccoyii*) are amongst the world's most highly migratory marine species (Maguire *et al.* 2006). The species has an almost circum-global pelagic distribution in the temperate southern latitudes between 30°S and 50°S (Fig. 1.1), yet displays a striking fidelity to a single spawning ground in the north-eastern Indian Ocean south of Java (between 7°S and 20°S) (Farley & Davis 1998). The single spawning ground, together with genetic (Grewe *et al.* 1997) and otolith microstructure (Proctor 1995) studies indicates the species constitutes a single stock. SBT are large (up to 2 m length and 200 kg weight), long-lived (up to at least 40 years) and late-maturing (age at 50% maturity is 10-12 years) (Caton 1991; Gunn *et al.* 2008). Like other tunas and billfishes, SBT possess significant morphological and physiological adaptations

for their lifestyle as pelagic predators including efficient and rapid swimming, high aerobic and anaerobic capacities, high metabolic rates, efficient food processing and storage and sensitive sensory systems (for reviews see Dickson 1995; Brill 1996). Of all Scombridae, the bluefin group posses the greatest capacity for endothermy, *i.e.* the ability to maintain body temperatures above ambient, through a highly evolved counter-current circulation system (Carey & Teal 1969; Carey 1973; Sharp & Dizon 1977). Hence, bluefin have the broadest thermal niche and most poleward range (Block *et al.* 1993).

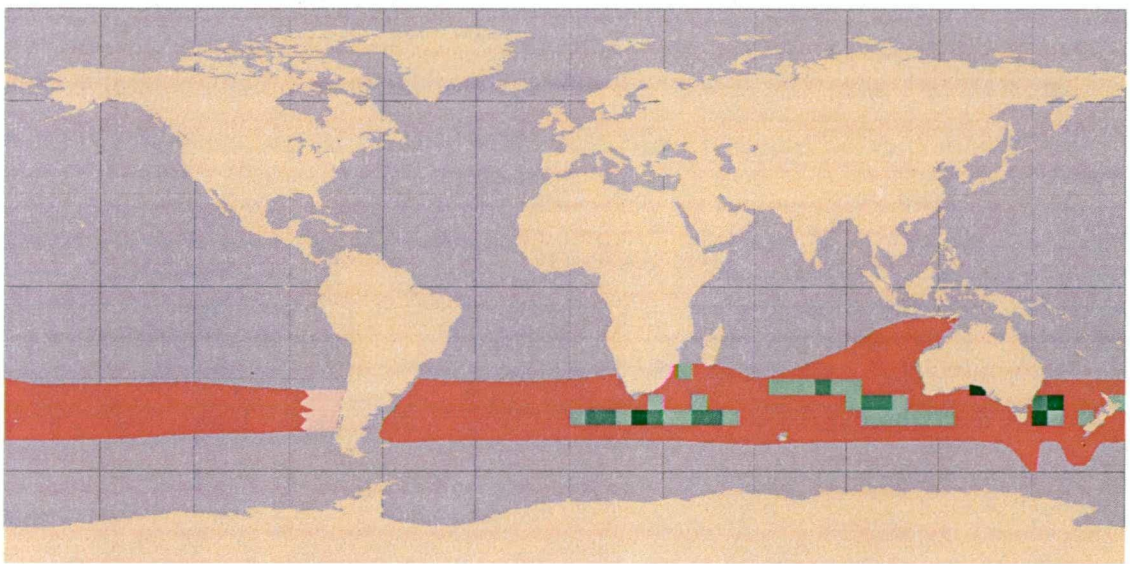

Fig. 1.1. General global geographic distribution of southern bluefin tuna (red = known, pink = uncertain) and main fishing grounds (green) reproduced from Maguire et al (2006). Main fishing grounds identified as 5 x 5° squares with the highest (> 250 tonnes) yearly average catches from all fishing gears for the period 2000-2005. Map courtesy of Fabio Carocci at FAO, Rome.

Exploitation and management

The life-history characteristics of SBT render the species especially vulnerable to over-exploitation and it was red-listed by the IUCN in 1996 as critically endangered, *i.e.* facing an extremely high risk of extinction in the wild, based on both abundance and exploitation indices[1]. Commercial exploitation of SBT commenced in the early 1950s with pole-and-line, later purse-seine, fishing

[1] http://www.iucnredlist.org/search/details.php/21858/summ accessed 28 April 2008.

targeting surface schools of juvenile fish in Australian coastal waters. The high-seas Japanese longline fishery commencing at a similar time (Caton 1991). The longline harvest peaked above 75 000 t in 1960-61 and declined steadily thereafter, resulting in a long-term spatial and temporal contraction of fishing effort (Campbell 1998). Australia, New Zealand and Japan voluntarily agreed the first global catch quota in 1986, and since 1994 the species has been managed under the international Commission for the Conservation of Southern Bluefin Tuna (CCSBT) whose stated objective is to rebuild the SBT spawning stock to the 1980 level by 2020. Current assessments estimate the parental biomass to be at historically low levels, 3–14% of it's pre-exploitation level (Basson *et al.* 2004). However today's international SBT fisheries are collectively worth around US$0.75 billion p.a. In addition, recent reviews of market data suggests catches may have been substantially under-reported over the past 10 to 20 years [2].

Migration dynamics

SBT have a multi-phase ontogeny with a spatially and temporally discrete set of migratory movements in each phase (Fig. 1.2; Caton 1991). Larval fish move from the spawning ground down the west coast of Australia, potentially drifting within the southward-flowing Leeuwin Current, to the coastal shelf waters of south-west Western Australia where fish aged 1 and 2 years old are common in surface catches. Further east in the Great Australian Bight, and historically as far as New South Wales, juvenile fish 2-5 years old are targeted by a surface purse-seine fishery during the austral summer (December-March) and older fish are uncommon. However, the occurrence of 2-4 year old SBT on the opposite side of the Indian Ocean during the austral summer indicates that juveniles are not restricted to Australian coastal waters and that a divergent migration path must exist, possibly near the southern west coast of Australia (Murphy 1977; Farley *et al.* 2007). Adult fish are mainly found feeding within the southern oceans in the region of the West Wind Drift (35 - 45°S).

[2] Global catch data from http://www.ccsbt.org/docs/data.html accessed 30 April 2008.

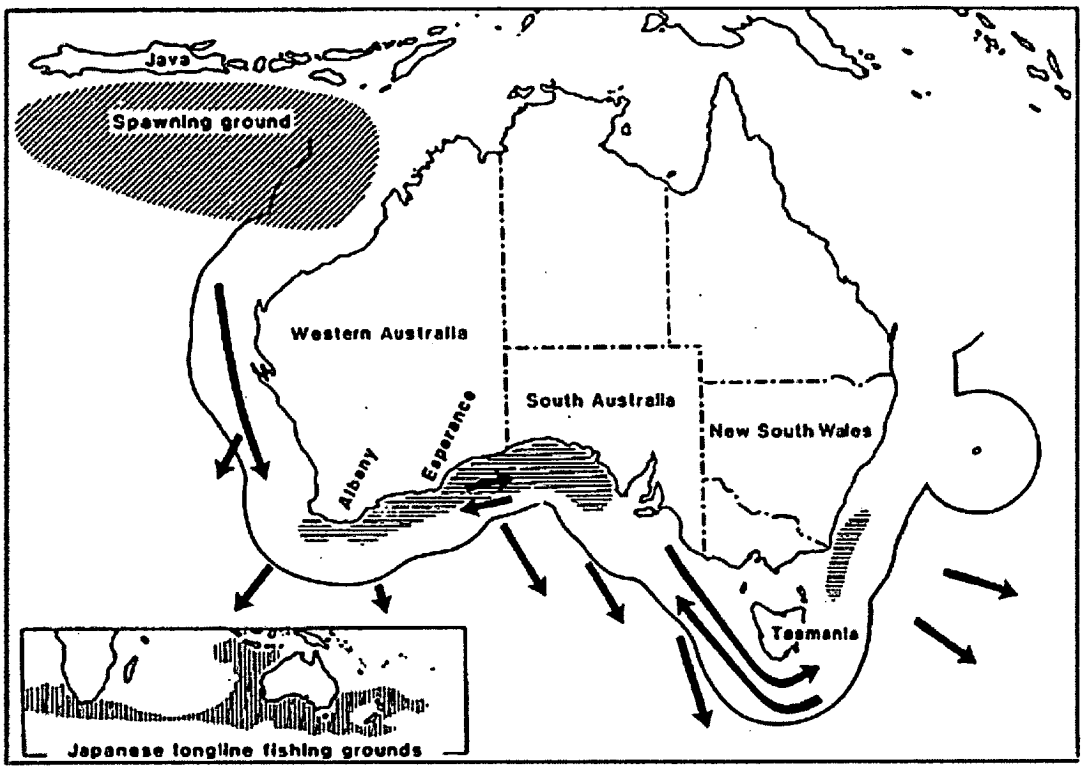

Fig. 1.2. Migration dynamics of southern bluefin tuna within and out of Australian waters, reproduced from Caton (1991). Hatching indicates the general distribution of the historical Australian surface fishery (horizontal hatching), now centred largely within South Australian shelf waters, and Japanese longline fishery (vertical hatching in inset panel). Also shown is the single spawning ground (diagonal hatching) and the Australian 200-mile exclusive economic zone (solid line).

Like with many other species of high market value, the fundamental age-specific movements and migration routes of SBT were originally elicited from the spatial and temporal distribution of the fishing grounds, and conventional tag-recapture experiments. The latter data, being fishery dependent, are also inherently biased by the fleet operations and differential reporting rates amongst fleets, and can give no information on intermediate movements between release and recapture. Juvenile fish were previously thought to progressively recruit (from 3 years old) to the high-seas. The development of a (on-going) large-scale electronic tagging program during the 1990's (Gunn *et al.* 1994) revealed that following their austral summer residency in Australian shelf waters, juvenile fish undertake a long-distance seasonal return migration into the Southern Ocean (Appendix A; Gunn & Block 2001). The commercial catches of SBT, patchy

across the species range (Fig. 1.1), are today dominated by juvenile and sub-adult fish on most longline fishing grounds in the southern oceans (Farley *et al.* 2007).

The seasonal migrations of juvenile SBT are thought to be feeding migrations, with inshore movements directed at exploiting seasonally abundant prey (Young *et al.* 1996; Young *et al.* 1997; Gunn & Block 2001) and offshore movements reflecting a wider dispersal in search of prey. However few studies have examined their feeding ecology and these have only been able to provide information at a spatially and temporally restricted scale relative to the species range (Serventy 1956; Robins 1963; Talbot & Penrith 1963; Young *et al.* 1997). In general, all bluefin species are known as opportunistic feeders capable of exploiting a wide variety of resources including pelagic fish, squid and crustaceans; and particularly for juvenile bluefin, zooplankton and micronekton (Young *et al.* 1996; Young *et al.* 1997; Estrada, Lutcavage & Thorrold 2005; Sara & Sara 2007). Dietary shifts have been observed over the course of a season, due to the use of different habitats, and in relation to ontogenetic changes (Young *et al.* 1997; Estrada *et al.* 2005; Sara & Sara 2007).

The life-history characteristics of southern bluefin tuna mean juveniles of the species are an excellent candidate for studying migrations of a large predator within a dynamic marine system. The synchronized annual life cycle means that during their coastal summer residency within the Great Australian Bight they are accessible for study and the deployment of electronic data storage tags, and vulnerable to recapture by commercial fishing operations. Extensive liaison with the fishing industry (Gunn *et al.* 1994; Gunn & Block 2001) has facilitated high rates of tag reporting and therefore data return. The annual oceanic migrations, being for non-breeding purposes, enables the study of their behaviours while foraging. Finally, in temperate tunas the physiological response to feeding produces a pattern of visceral warming that is measurable by a temperature sensor surgically implanted within the body cavity (Carey, Kanwisher & Stevens 1984; Gunn, Hartog & Rough 2001). This provides a record of when feeding occurs and enables linkages between feeding, movement and environment to be directly examined.

Chapter 1

MARINE PREDATORS AND THEIR ENVIRONMENT

Researchers in many disciplines have long attempted to link the distribution, abundance, behaviour and migratory activity of a range of top predators across taxa to oceanographic features and patterns of productivity in the marine environment. Within the highly variable marine environment the distribution of biological resources is heterogeneous and patchy, both spatially and temporally, with many physical processes determining the distribution of nutrients and hence primary productivity (Lutjeharms, Walters & Allanson 1985; Moore & Abbot 2000; Mann & Lazier 2005). Productivity is often concentrated in coastal/shelf areas and around other bathymetric or oceanographic features such as upwelling zones, frontal features of convergence or divergence, or sea-ice margins. Increased productivity provides energy transfer through marine food webs to higher trophic levels, via zooplankton and their consumers (micronekton, fish and squid) to top-order predators.

Particularly for species of high market value there has been strong incentive for identifying what constitutes good "fishing habitat", *i.e.* areas where predictable concentrations of (feeding) predators may be found. Historically, for tunas and tuna-like species efforts were often directed towards identifying optimal or preferred temperature ranges (Clemens 1961; Blackburn 1969; Sund, Blackburn & Williams 1981) and regions of frontal activity (Shomura & Otsu 1956; Shingu 1978) typically predictive of fish habitat. Vertical structure, such as the depth of the mixed layer and strength of the thermocline, were also of interest (Laurs & Lynn 1977). Much of the early information came from relatively few measurements of oceanic conditions from research surveys or commercial vessels, but from such scarce information in combination with ever-expanding fleet movements a great deal of the basics of animal distribution, movement and behaviour was pieced together (for reviews on bluefin species see Caton 1991; Bayliff 1994).

A significant advancement in identifying animal-environment linkages was the development of remote-sensing, providing synoptic measurements of various physical attributes such as sea surface temperature, and more recently

ocean colour (from which phytoplankton concentration can be estimated), and sea surface height anomalies (which can provide good indication of areas of mesoscale activity, *e.g.* eddies and frontal zones). Significant insight has been gained from qualitatively examining satellite maps in combination with other biological data, such as fine-scale acoustic tracking of animals (Laurs, Yuen & Johnson 1977; Brill *et al.* 2002; Davis & Stanley 2002). At regional scales data from abundance surveys (Royer, Fromentin & Gaspar 2004), fishery catches (Zainuddin, Saitoh & Saitoh 2004) and electronic tracking (Nel *et al.* 2001; Polovina *et al.* 2006; Cotte *et al.* 2007) are increasingly highlighting the importance of mesoscale oceanographic features to marine predators. The synoptic global coverage of remote-sensing, together with larger-scale and better quality electronic tagging data, is further revealing ocean basin-scale patterns in predator movements and the oceanographic features underpinning those movements (Lehodey *et al.* 1997; Polovina *et al.* 2001; Shaffer *et al.* 2006; Biuw *et al.* 2007).

The near-surface circulation of the temperate south Indian Ocean is dynamic and complex (McCartney 1982; Nagata, Michida & Umimura 1988; Belkin & Gordon 1996; Read *et al.* 2000; James *et al.* 2002; Kostianoy *et al.* 2004; Yuan, Martinson & Dong 2004; Lutjeharms 2007), dominated by a series of major circumpolar fronts separating a number of belts of water with quasi-uniform water mass properties (Fig. 1.3). The transition between the warm, saline subtropical waters and the subantarctic zone is marked by strong meridional gradients in temperature and salinity, and strong westerly winds drive the circumpolar currents eastward. In the south-west of the basin, the bottom topography exerts strong control over the eastward-flowing currents and the close juxtaposition of fronts creates intense mesoscale activity. These oceanographic properties provide a diversity of habitats that influence the distribution, diversity, and abundance of the biological communities they support (Pakhomov & McQuaid 1996; Ansorge *et al.* 1999; Pakhomov *et al.* 2000; Read *et al.* 2000), although relatively little is known about mid-trophic organisms such as fish and squid (Cherel, Duhamel & Gasco 2004; Cherel & Hobson 2005; Collins & Rodhouse 2006). During an annual migration juvenile SBT may therefore be

expected to encounter oceanic habitats with widely varying physical and biological characteristics.

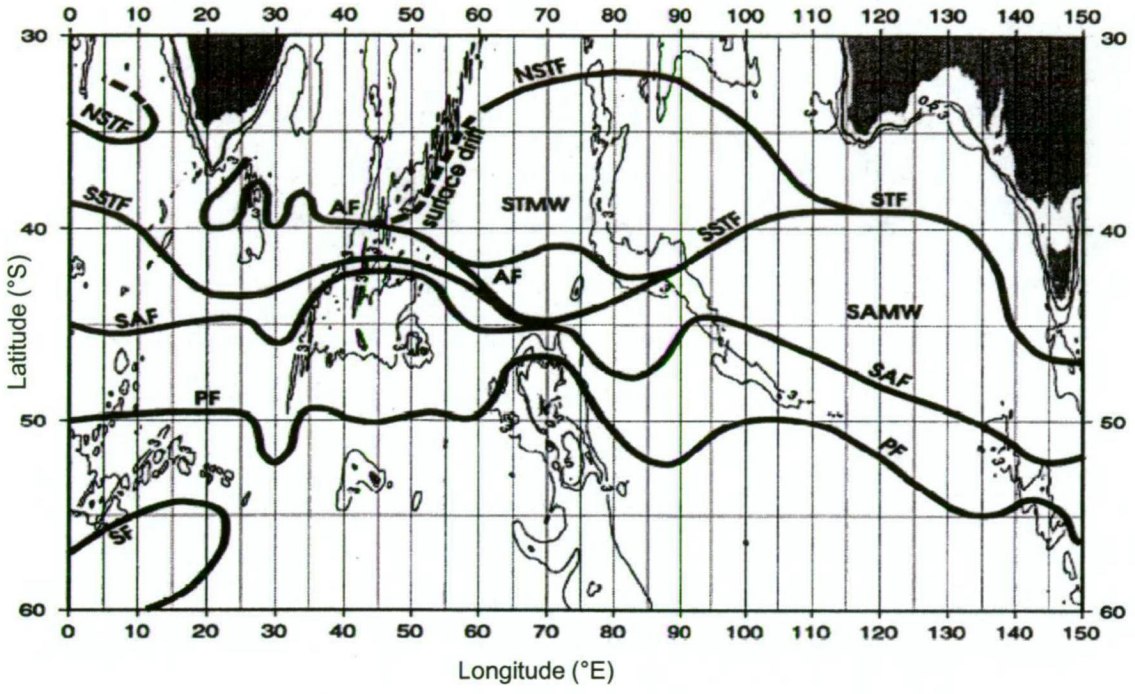

Fig. 1.3. The climatological frontal structure of the south Indian Ocean (reproduced from Belkin and Gordon, 1996). STF – sub-tropical front, SAF – sub-Antarctic front, PF – polar front, AF – Agulhas front, NSTF and SSTF – north and south sub-tropical fronts respectively. The sub-tropical mode water and sub-Antarctic mode water areas are roughly indicated by STMW and SAMW respectively. Background shows bottom topography (0.5, 1 and 3 km isobaths).

Chapter 1

The integration of oceanographic and biological disciplines is a dynamic area of research, in part due to technological developments and increased capacity driving improved science. The electronic tagging technology is increasingly sophisticated (for reviews see Gunn & Block 2001; Cooke *et al.* 2004; Ropert-Coudert & Wilson 2005), with better tags deployed in larger numbers providing ever more detailed information on individual movement and diving behaviour, as well as often collecting environmental (*e.g.* water temperature, salinity) and physiological information (*e.g.* heart rate, body temperature). Of particular value is the development of methods for remote monitoring of feeding activity, most commonly via stomach or esophageal temperature (Wilson, Cooper & Plotz 1992; Gales & Renouf 1993; Austin *et al.* 2006a; Bost *et al.* 2007), but also for example using jaw angle (Liebsch *et al.* 2007), stomach pH (Papastamatiou & Lowe 2005), buoyancy (Biuw *et al.* 2003) and echolocation (Watwood *et al.* 2006). Direct feed indices avoid the need for proxies of foraging behaviour, such as changes in space-use, movement or diving patterns, which are often non-trivial to develop and further may provide information on search effort rather than success.

Electronic tagging data does however present a number of challenges. Large volumes of high resolution data are provided, often on relatively few individual animals, and interpreting patterns can be extremely difficult. It is important to both characterize the variation among individuals, and plasticity in behavioural responses, yet develop a synthesis of general patterns appropriate to populations or broader ecological scales. Further, the time-series nature of the data collection, representing repeated sampling from the same individual, requires relatively complex statistical analysis if relationships between animal behaviour (*e.g.* swimming depth, feeding success) and environmental influences are to be quantified. While this autocorrelation is often treated as a nuisance (or ignored), valuable ecological insight can in fact be obtained from quantifying both the nature of the time-dependence and the effect of individuals. The approaches explored in this thesis form part of the ongoing development of more sophisticated and useful analytical approaches for research integrating animal ecology with their physical environment using telemetry-based data.

AIMS AND THESIS STRUCTURE

Movement is a fundamental component of an individual's life and a species natural history. The movement paths of individuals and populations reflect both ecological and evolutionary responses to environmental heterogeneity. The overarching aim of this thesis is to improve our understanding of proximate environmental influences on the long-distance migration dynamics of a pelagic predator, juvenile southern bluefin tuna. Since their migrations are not for the purposes of spawning, juveniles represent a good study candidate for examining direct linkages between environmental factors and movement, swimming behaviour and foraging success. These linkages are explored through the integration, analysis and interpretation of telemetry-based and oceanographic data, for which a number of novel approaches are developed. This thesis is organized into four research chapters and the findings drawn together in a final synthesis chapter. I present data and analyses for:

Seasonal ocean processes

Chapter 1 tests the hypothesis that juvenile southern bluefin tuna undertake their long-distance directed migrations to regions where environmental conditions are favourable for food production. An oceanographic technique, empirical orthogonal function (EOF) analysis, is applied to remotely-sensed fields of ocean temperature and ocean colour to extract the dominant modes of environmental variability. This is used in combination with tracking data from individual SBT carrying archival tags to (1) examine the large-scale ocean dynamics and patterns of biological production within the south Indian Ocean, and (2) investigate the correspondence between seasonal oceanic processes and productivity and the destinations of migrating fish. This approach places the animal movements within the spatial and temporal context of the ocean environment at an ocean basin scale.

Plasticity in vertical behaviour

Chapter 2 aims to (1) characterise the three-dimensional oceanographic habitats used throughout a migration cycle on the basis of water column structure (using

fine-scale temperature-at-depth data from archival tags), and (2) quantitatively test whether and how the vertical behaviour patterns of SBT altered between different habitat types and also in response to diel period, lunar phase and migration status. Variability within and between individuals is quantified. The highly plastic behaviours displayed in response to the changing ocean environment are discussed in light of the possible proximate causes of the observed changes, *i.e.* prey distribution, and with reference to the significant challenges posed for the interpretation of fishery data used in stock assessments.

Feeding and foraging ecology

Chapter 3 examines the temporal feeding patterns and seasonal foraging ecology of juvenile southern bluefin tuna. Direct information on feeding activity is obtained from visceral warming patterns recorded by archival tags implanted within the body cavity. Specifically, the hypothesis that highly mobile species should spend more time in energetically profitable areas is tested, by examining the relationship between feeding success and time spent in an area. Observed trends are discussed in terms of both predator search strategies and alternative reasons that may motivate residency.

Factors predictive of feeding success

Chapter 4 provides an appropriate statistical method to model feeding as a time-dependent (Markov) process, with the aim of determining what environmental characteristics are predictive of high foraging success for migratory juvenile southern bluefin tuna. The models integrate data on ocean temperature collected by the tags, data on oceanic productivity collected by satellites, and a number of other environmental covariates. The results provide insight into the nature of the benefit gained from the seasonal occupation of the coastal Great Australia Bight and also a new perspective on migration models appropriate for opportunistic predators in the heterogeneous open ocean environment.

Synthesis and conclusions

Chapter 6 integrates the results obtained from the preceding four research chapters. Although in each chapter the results are interpreted within a broad ecological context, this discussion provides a synthesis of the findings with respect to three major thematic areas that repeatedly arise throughout the work, and that lead to generalisations potentially applicable across other species and studies: (1) linkages between biology and oceanography; (2) habitat use versus foraging, and (3) behavioural flexibility, individual variability and predictability. Finally, future research directions are proposed.

Thesis structure

This thesis has been written as a series of separate manuscripts with a number of co-authors from the Antarctic Wildlife Research Unit, IRD Centre de Recherche Halieutique, and CSIRO Marine and Atmospheric Research. All chapters, with the exception of this introductory and a final synthesis/conclusions chapter, comprise a manuscript in preparation or an already submitted or accepted paper for publication. In consequence, some textual overlap occurs in these chapters. While I have been the senior author for each of the papers and was responsible for the data analyses and interpretation and the preparation of manuscripts, the contribution of the co-authors was either in organising the collection of data, data analysis, or in the preparation of manuscripts for publication. The co-authors are listed with the title at the start of each chapter, and their contribution detailed in the statement of publication and co-authorship. A single bibliography is presented at the end of the thesis adopting the referencing style of Journal of Animal Ecology.

2. Influence of seasonal ocean dynamics on the migrations of juvenile southern bluefin tuna

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ABSTRACT

The annual long-distance migrations of juvenile southern bluefin tuna (*Thunnus maccoyii*, SBT) were examined within the context of the large-scale seasonal ocean processes of the south Indian Ocean. In particular, we investigated whether SBT migrate to regions where environmental conditions are favourable for food production. Our analysis of remotely-sensed sea surface temperature (SST) and sea surface colour (SSC), in combination with tracking information from a large-scale archival tagging experiment, identified three primary oceanographic features in the south Indian Ocean, and their cycle of development and/or primary productivity, that may provide important seasonal feeding habitats for juvenile SBT. These were (1) the southern margin of the subtropical gyre, (2) the region of mode water formation in the central-eastern basin, and (3) the Agulhas retroflection system in the south-western basin. In at least two of these environments, the timing of SBT migrations coincided with enhanced seasonal primary production, which potentially provides the basis for the development of pelagic trophic webs and therefore trophic transfer to higher order predators. This study demonstrates how the multi-disciplinary approach integrating oceanographic and biological data can provide new insights into the motivations for movement and the specific timing and spatial extent of long-distance oceanic migrations.

Keywords: Bluefin tuna; South Indian Ocean; Biotelemetry; Migratory species; Feeding migrations.

Chapter 2

INTRODUCTION

Southern bluefin tuna (*Thunnus maccoyii*, hereafter SBT) are one of the world's most migratory fishes. SBT have a single spawning ground in the tropical Indian Ocean south of Indonesia, to which adult fish make long-distance migrations from their feeding grounds in the temperate latitudes (30-50°S) of the Pacific, Indian and Atlantic Oceans (Caton 1991). Juvenile SBT are also highly migratory, inhabiting the shelf waters of southern Australia during the austral summer, and then dispersing widely into oceanic waters (Polacheck, Hearn & Whitelaw 1996). An extensive archival tagging program (Gunn *et al.* 1994; Gunn & Block 2001) has shown these movements are in fact regular, return migrations undertaken by juvenile fish each year. While a proportion move eastward into the Tasman Sea, the majority undertake highly directed, long-distance migrations westward into the south Indian Ocean (Gunn & Block 2001).

The motivation for such long-distance migrations is unknown. Northcote (1978) suggested that fish migration has evolved (1) to optimize feeding, (2) to avoid unfavourable conditions, (3) to enhance reproductive success and/or (4) possibly to promote colonization. As we are considering premature fish of a species not known to form permanent resident populations, we can discount (3) and (4). With respect to (2), one explanation might be that winter storms and associated wind-driven overturning and turbidity in the shelf waters of the Great Australia Bight adversely impact SBT and/or their prey. Yet to avoid such unfavourable conditions SBT could elect to simply migrate a relatively short distance into offshore waters as commonly observed in juveniles of other tuna species (Itoh, Tsuji & Nitta 2003a; Block *et al.* 2005; Wilson *et al.* 2005). The highly directed and long-distance nature of their migrations is not explained by this scenario alone. The evolution of a migratory behaviour must confer some advantage (or at least not confer a disadvantage) for a species to maintain itself within such an ecological niche. For a juvenile fish, improved feeding and growth (*i.e.* a strategy evolved to maximize foraging and/or survival in a vast and naturally heterogeneous pelagic environment) may account for the migratory behaviour. If it is the case that SBT are not merely migrating to an "over-

wintering" ground, but to an alternate "feeding" ground(s), the timing of the migration patterns should have evolved such that the fish arrive at areas where environmental conditions are favourable for food production.

Animals carrying archival tags provide us with the opportunity to understand the movements and residency of these highly mobile large pelagic predators directly within the context of their bio-physical environment (Block *et al.* 2003). Remotely-sensed fields of ocean temperature and colour give an indication of ocean conditions and near-surface biological productivity, and empirical orthogonal function (EOF) analysis (Lorenz 1956; Kutzbach 1967; Davis 1976; Venegas 2001) can be used to extract the dominant modes of environmental variability. The combined use of these approaches enables the identification of oceanographic features that could affect habitat suitability or biological productivity and thus influence animal distributions. The aim of this study was therefore to test the hypothesis that juvenile SBT undertake their long-distance directed migrations to regions where environmental conditions are favourable for food production. Specifically, we use a combination of individual tracking data and remotely-sensed data to (1) examine the large-scale ocean dynamics and patterns of biological production within the south Indian Ocean, and (2) investigate the correspondence between seasonal oceanic processes and productivity and the destinations of migrating SBT.

METHODS

Environmental data

Sea surface colour (SSC, chlorophyll-a concentration in mg m^{-3}, grid resolution 0.0833 x 0.0833 degree, or 9 km) as measured by the satellite-borne SeaViewing Wide-Field of View Sensor (SeaWiFS) was obtained from the NASA Goddard Space Flight Centre (http://oceancolor.gsfc.nasa.gov). Sea-surface temperature (SST, Optimum Interpolation V2, grid resolution 1.0 x 1.0 degree) and zonal surface wind (ZSW, NCEP Reanalysis, grid resolution 2.5 x 2.5 degree) data were obtained from the NOAA/OAR Earth System Research Laboratory (http://www.cdc.noaa.gov). Maps of sea-level anomaly (SLA, merged Topex/Poseidon-ERS data, grid resolution 1.0 x 1.0 degree) were produced by the CLS Space Oceanography Division with support from CNES (http://www.cls.fr). The ZSW and SLA data although not included in the EOF analysis provide supplementary information on Indian Ocean dynamics.

Monthly data were used for all parameters between September 1997 and August 2002 (60-months). To examine open-ocean processes, the focus region was restricted to between 30°E and 110°E, thereby avoiding coastal influences in the vicinity of Africa and Australia. South of 45°S, satellite coverage of SSC in the austral winter and spring months was heavily reduced due to persistent cloud cover, so the analysis was restricted to the latitudes 27.5–45°S. Relatively few SSC pixels were missing within this domain (mean ± S.D: 2.7% ± 1.3%, range = 0.4–5.5% per monthly image) and these were filled by kriging. The complete set of SSC images was split into 4 seasons: spring (September to November), summer (December to February), autumn (March to May) and winter (June to August). Spherical variograms models were fitted for each season and applied on each image, for the corresponding season, in the krigging procedure. The krigged SSC data were then re-gridded to a 1.0 x 1.0 degree grid to match the spatial resolution of the SST fields. SeaWiFS 8-day composites at the original 9-km resolution are shown for the case studies of individual fish.

The SSC data were log-transformed prior to the EOF analysis. To remove any geometric artefact of latitude density, all data were weighted by the cosine of latitude. To produce seasonal SST and SSC anomalies (centred anomalies) the long-term (60-month) temporal mean was subtracted at each (1.0° x 1.0°) pixel location. Normalized and non-normalized series were both examined. For normalization, each (centred) data point was divided by the standard deviation of the time-series at that pixel location, which ensures the analysis is not dominated by the variability from any given location (Venegas 2001). Normalization made a negligible difference however, thus only the results from the non-normalized series are displayed.

EOF analysis

Empirical orthogonal function (EOF) analysis (Lorenz 1956; Kutzbach 1967; Davis 1976; Venegas 2001) of the SST and SSC data sets was used to determine the characteristic patterns of variability. The EOF analysis provides a compact description of the spatial and temporal variability in a data series in terms of orthogonal functions, or statistical "modes". Usually, most of the variance is described in the first few orthogonal functions, whose patterns may form some link to dynamical mechanisms. Singular value decomposition (Venegas 2001) was used to obtain eigenvalues, eigenvectors and time-varying amplitudes (principal components, see Appendix A).

Archival tag data

The archival tag data used in this study form part of an extensive and ongoing program tagging juvenile SBT in the Great Australia Bight (Gunn & Block 2001). During the austral summers of 1998–2000 two hundred SBT were caught by pole-and-line and archival tags of model Mk7 (Wildlife Computers, Redmond, WA) were surgically implanted into the peritoneal cavity ventral to the stomach (Gunn *et al.* 1994). The archival tags were set to Greenwich Mean Time (GMT) and programmed to sample the pressure, ambient light, and water and visceral temperatures every 4 minutes (for full specifications see http://www.wildlifecomputers.com). To date, 51 tags (26%) have been recovered,

and data downloaded successfully from 47. Only short-term data sets were available from 18 of these due to early recapture (n = 10), or very early sensor (n = 4) or tag (n = 4) failure. The remaining 29 tags provide excellent long-term (*i.e.* > 120 days) data sets. Daily longitudes were determined using proprietary light-based geolocation software (GeoControl v2.01.0002; Wildlife Computers, Redmond, WA) relating the mid-point between sunrise and sunset to Greenwich Mean Time (Hill 1994). The accuracy of the longitudes were validated as far as possible by comparing the reported release and recapture locations with the nearest available position estimate (usually ± 2 days). The root-mean-square errors were 0.66° (n = 29) and 1.14° (n = 13) for release and recapture locations, respectively. These longitudes indicated that 19 fish (66%) moved predominantly west to the Indian Ocean (range = 35–147°E) during their first year at sea (Table 2.1).

There are well-documented problems in determining latitude from light-based geolocation (Welch & Eveson 1999; Hill & Braun 2001; Musyl *et al.* 2001) and increasingly, environmental data have been incorporated to improve position estimation, particularly satellite sea surface temperature data (Beck, McMillan & Bowen 2002; Itoh *et al.* 2003a; Teo *et al.* 2004; Domeier *et al.* 2005). We similarly estimated latitude by comparing the surface water temperature recorded by the archival tag with satellite SST estimates. Briefly, using the Multi-Channel SST (night passes) 8-day 18km interpolated product, a longitude strip centred on the geolocation longitude (±1°E) was searched from 20-60°S. We display here the median positions of all MCSST pixels matching within ±0.2°C of the median tag SST recorded in the surface 5m during each 24-hour period. Using this method the latitudinal range, *i.e.* the 90th percentile of all pixel matches, was less than 3.5 degrees latitude for 94% of all position estimates. The average 90th percentile boundaries were 1.06 and 0.84 degrees to the north and south of the median position respectively. Of the 2129 daily position estimates located in the south Indian Ocean (*i.e.* west of 110°E), 50 positions (2.3% of the available data) were located outside the domain latitudes described above and were excluded from the subsequent analysis.

Table 2.1. Individual release and recapture information for 19 tagged juvenile SBT which migrated westward from the Great Australia Bight into the south Indian Ocean during their first year at liberty.

	Release Information				Period within the South Indian Ocean (30–110°E, 27.5–45°S)					Recapture Information			
Tag Number	Date	LCF (cm)	Latitude (°S)	Longitude (°E)	First date	Last date	Days present	Position estimates available	Minimum Longitude (°E)	Date	LCF (cm)	Latitude (°S)	Longitude (°E)
97615	26-01-98	100	33.28	131.43	29-06-98	08-09-98 [F1]	72	68	53.73	07-07-01	125	39.62	28.52
97622	03-01-98	98	32.80	132.60	08-06-98	08-10-98	123	121	59.88	15-02-99	NA	33.25	131.23
97639	27-01-98	97	33.12	132.00	03-09-98	14-11-98	73	65	82.48	05-03-03	153[c]	33.43	131.75
97682	03-01-98	93	32.80	132.60	05-10-98	30-11-98 [F1]	57	46	77.21	09-01-99	NA	33.15	131.23
97708	03-01-98	97	32.80	132.60	31-07-98	06-09-98 [F1]	38	38	71.93	13-01-99	114	33.40	132.70
97718	26-01-98	98	33.28	131.43	19-07-98	21-08-98 [F1]	34	33	76.33	11-02-99	NA	33.58	131.57
97721	03-01-98	96	32.80	132.60	20-05-98	17-11-98	182	175	74.92	15-01-99	114[c]	33.35	131.82
97733	26-01-98	103	33.12	132.00	18-09-98	04-10-98	17	5	108.5	30-01-99	125[c]	33.47	132.03
97741	26-01-98	97	33.30	131.62	21-08-98	01-10-98 [L1]	42	38	78.35	29-07-00	121	39.13	156.47
98007	26-01-98	96	33.28	131.43	14-09-98	29-11-98	77	72	78.44	18-02-99	NA	33.92	132.12
97731	01-03-99	95	33.30	131.48	17-05-99	01-07-00	412	381	34.91	02-07-00	115	32.50	80.52
98553	01-03-99	111	33.30	131.48	05-06-99	25-01-00 [L2]	235	192	46.34	18-02-01	133[c]	33.88	132.52
98574	01-03-99	102	33.30	131.48	14-07-99	18-07-99	5	5	104.4	20-07-99	107	39.75	103.68
99267	17-02-00	100	33.57	132.15	01-06-00	18-12-00	201	194	75.71	24-06-01	118	39.80	154.67
99626	17-02-00	99	33.57	132.15	30-05-00	07-02-01 [F2]	254	248	35.88	19-06-02	134	32.30	87.50
99627	17-02-00	103	33.57	132.15	28-05-00	01-01-01	219	210	73.6	22-01-01	111[c]	33.50	131.92
99629	17-02-00	104	33.57	132.15	17-06-00	08-11-00 [T2]	145	143	69.47	09-01-02	NA	33.58	132.32
99630	18-02-00	106	33.57	132.15	29-04-00	07-01-01	253	57*	49.95	06-03-01	116[c]	34.18	132.77
99664	17-02-00	99	33.57	132.15	06-09-00	14-10-00 [F1]	39	38	78.79	17-11-01	116	40.92	37.18

[F, T, L] Indicates tag failure (F), light sensor (L) or external temperature sensor (T) failure

[1, 2] Failure occurred on outbound (1) and inbound (2) journey from/to the GAB

[c] Recapture length was reported after a period in Australian farm cages in the GAB; however within cages SBT largely gain weight rather than length (Carter *et al.* 1998)

* Tag 99630 suffered two extended periods of light-sensor failure (19-May-00 to 28-Sep-00 and 14-Oct–00 to 5-Dec-00) hence few geolocation positions are available

RESULTS

Oceanographic mean state and variability

The south Indian Ocean, even far from coastal boundaries, is a region of complex and dynamic oceanography. The transition between the warm, saline subtropical waters and the subantarctic zone is marked by strong meridional gradients in temperature (Fig. 2.1a) and salinity. Like elsewhere, the subtropical gyre is characterized by stratified surface waters with very low and limiting concentrations of nutrients and associated low primary productivity (Fig. 2.1b). South of 40°S is the region termed "the roaring forties", characterised by strong westerly winds driving circumpolar currents eastward, uninterrupted by land masses (Fig. 2.1c). In the south-western sector of the basin, the bottom topography exerts strong control over the eastward-flowing circumpolar currents, creating the intense mesoscale activity of the Agulhas retroflection system (Fig. 2.1d) and one of the most energetic and productive (Fig. 2.1b) regions of the world oceans.

The temperate seas display considerable physical-biological variability around the mean background state. The central and eastern (>70°E) basin is strongly perturbed by the seasonal cycle of cooling (warming) surface temperatures (Fig. 2.2a) and strengthening (slackening) of zonal winds (Fig. 2.2c) during the austral winter (summer). At this time the surface cooling and wind-driven overturning in this region deeply mixes the upper water column to form an homogeneous layer termed mode water (McCartney 1982). The strongest variability in ocean colour is observed along the southern margin of the subtropical gyre (Fig. 2.2b). There is little seasonal variability in SLA patterns, with highest energies consistently found in the Agulhas retroflection (Fig. 2.2d).

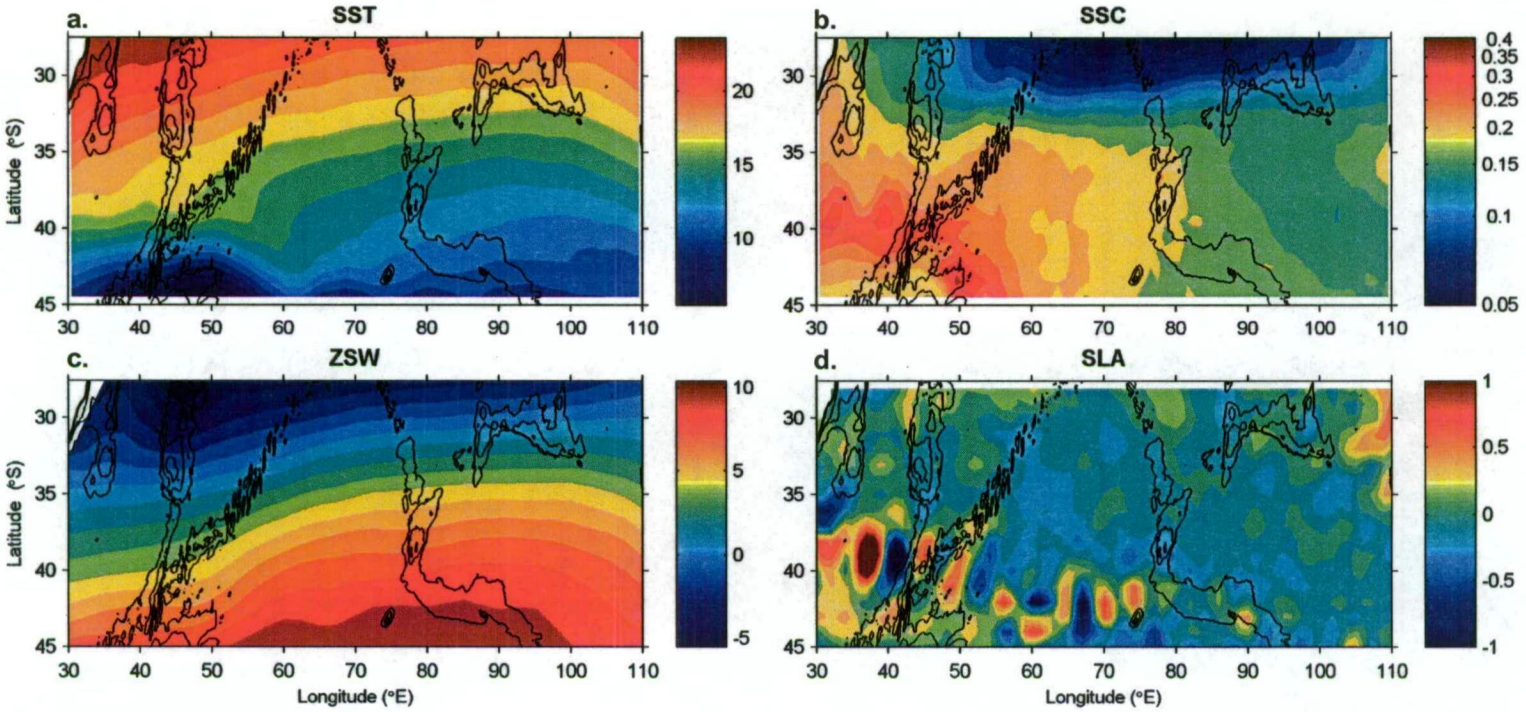

Fig. 2.1. The oceanographic mean state in the south Indian Ocean. (a) Sea surface temperature (°C), (b) sea surface chlorophyll (mg m^{-3}), (c) zonal surface wind (m s^{-1}, positive eastward), and (d) sea-level anomaly (m). Based on monthly-averaged, 1-degree resolution fields for the 60-month period September 1997 – August 2002. Contours show the 0 m, 1000 m, 2000 m and 3000 m isobaths (TerrainBase bathymetry from the National Geophysical Data Centre, http://www.ngdc.noaa.gov).

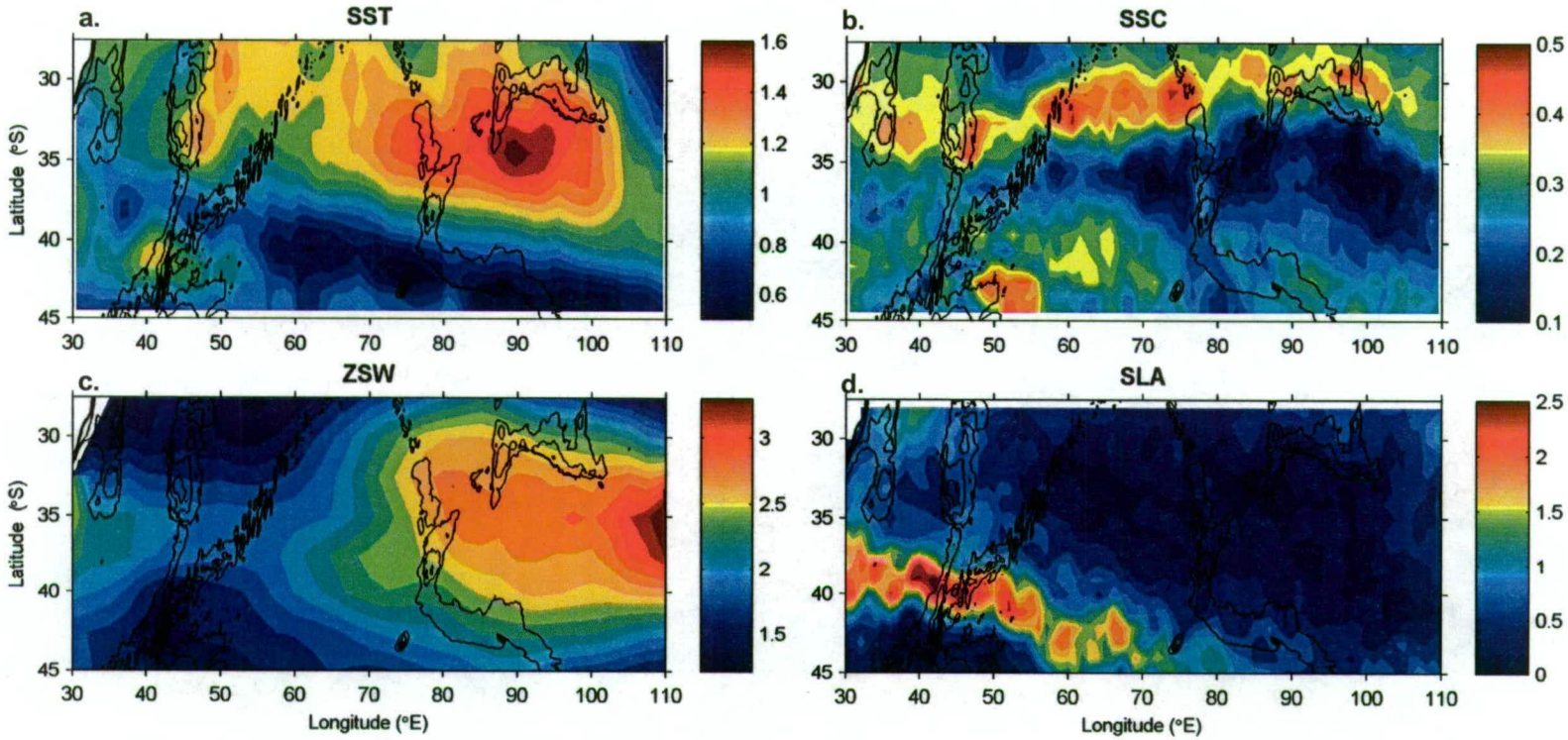

Fig. 2.2. Physical-biological variability in the south Indian Ocean. Standard deviation of (a) sea surface temperature (°C), (b) sea surface chlorophyll (mg m^{-3}), (c) zonal surface wind (m s^{-1}), and (d) sea-level anomaly (m).

Seasonal EOF modes

The EOF decomposition of monthly SST and SSC fields reveals the dominant spatial patterns of variability. In the SST field, the first mode explains 92% of the variance in the data set, and shows the characteristic annual cycle of warming and cooling (Fig. 2.3a). The seasonal anomaly is of greatest magnitude in the central-eastern basin (70–90°E), as noted above, and within mid-latitudes (32–37°S). The second mode (not shown) explains only 3% of the variance and describes a periodic feature that is non-seasonal (*i.e.* an oscillation of >12 months). In the SSC field the first two EOF modes describe 60% and 12% of the variance respectively, and both modes describe seasonal patterns. The dominant mode describes a north-south contrast, with the maximum reached around July-September *i.e.* mid-winter, and the minimum occurring in January-March *i.e.* mid-summer (Fig. 2.3b). Across the entire basin along the subtropical margin (between ~30–35°S) the surface chlorophyll is enhanced in the winter months relative to the summer months (this region is coloured with a positive anomaly). In contrast, most of the region south of this shows higher chlorophyll during the summer months relative to the winter months (this region is coloured with a negative anomaly). The second mode (Fig. 2.3c) describes a specific peak in surface chlorophyll during spring-early summer (October – January, maximum occurring in November). The strongest enhancement occurs within the Agulhas retroflection region in the western basin (maxima ~40–60°E, 35–40°S) and extends from here along the boundary between the northern and southern zones described by mode 1.

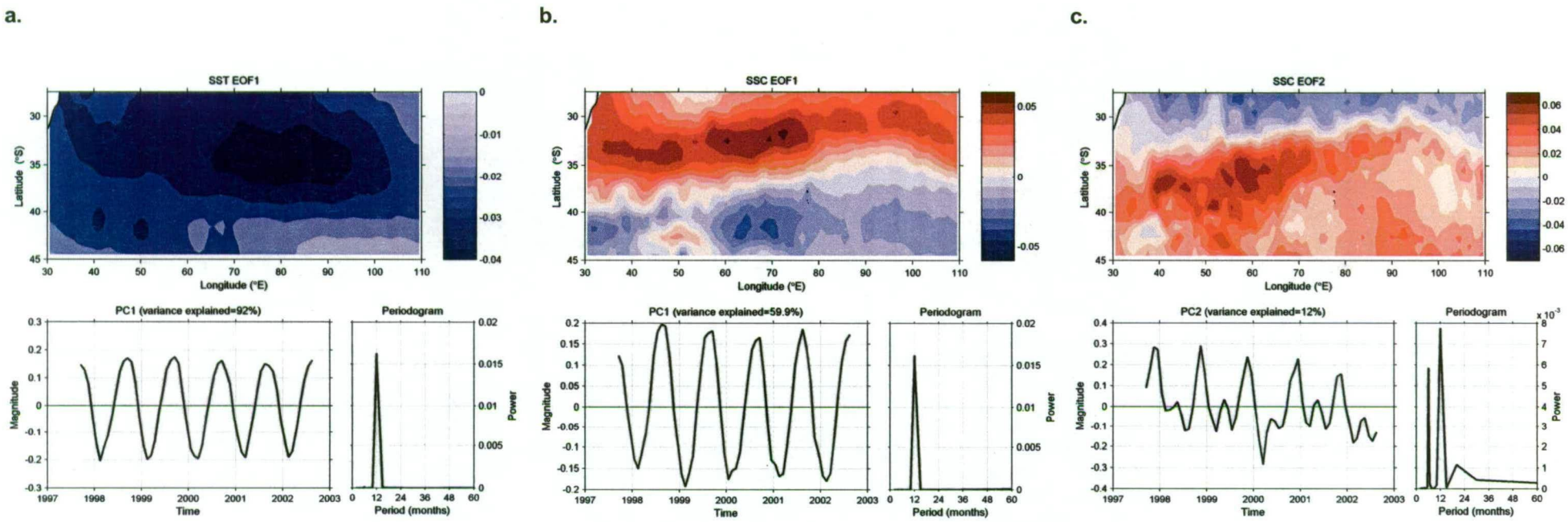

Fig. 2.3. EOF decomposition of monthly SST and SSC. (a) The first SST mode, and (b) the first, and (c) second SSC modes. Panels in the bottom row show the corresponding principal component time-series (LHS) and spectral analysis of the time-series showing the periodicity of the signal (RHS).

Tuna movement and behaviour

The correspondence between SBT movements and the physical processes identified in the EOF analysis is shown in Fig. 2.4. The presence of SBT in the south Indian Ocean appears largely in phase with the cycle of seasonal cooling, *i.e.* positive phase SST EOF mode 1 (Fig. 2.4a), although there is variability between individual fish (Table 2.1, Fig. 2.4c). For example, a notable exception to this pattern is the single fish which did not return to the GAB but remained in the south Indian Ocean throughout early 2000 until being recaptured in July (SBT97731, Fig. 2.4c). There also appears to be some degree of interannual variability, with fish tagged in 2000 arriving in the south Indian Ocean somewhat earlier and leaving later than the fish tagged in 1998 (mean arrival and departure dates in 1998: 5 August – 3 November; in 2000: 14 June – 2 January).

The presence of SBT within the south Indian Ocean also coincides with the positive phase of the two dominant EOF modes identified in the SSC analysis (Fig. 2.4b), although an association with the spring peak (described by EOF 2) appears more notable for those few SBT migrating into the western basin. Time-latitude diagrams of SBT movements and chlorophyll-a concentration illustrate the different phase relationships between the eastern and western ocean basins (Fig. 2.5). In the western basin (Fig. 2.5a) SBT focussed largely south of 35°S in waters of very high SSC, during prolonged residencies extending through spring and into early summer. In comparison in the eastern basin (Fig. 2.5b) SBT were widely distributed during winter-spring, the period of northward expansion of the surface chlorophyll zones. Association with the spring-summer enrichment in the southern latitudes of this region is not a prominent feature. SBT do however occur in these southern latitudes in the winter, in no apparent association with zones of surface chlorophyll enrichment or frontal contrasts.

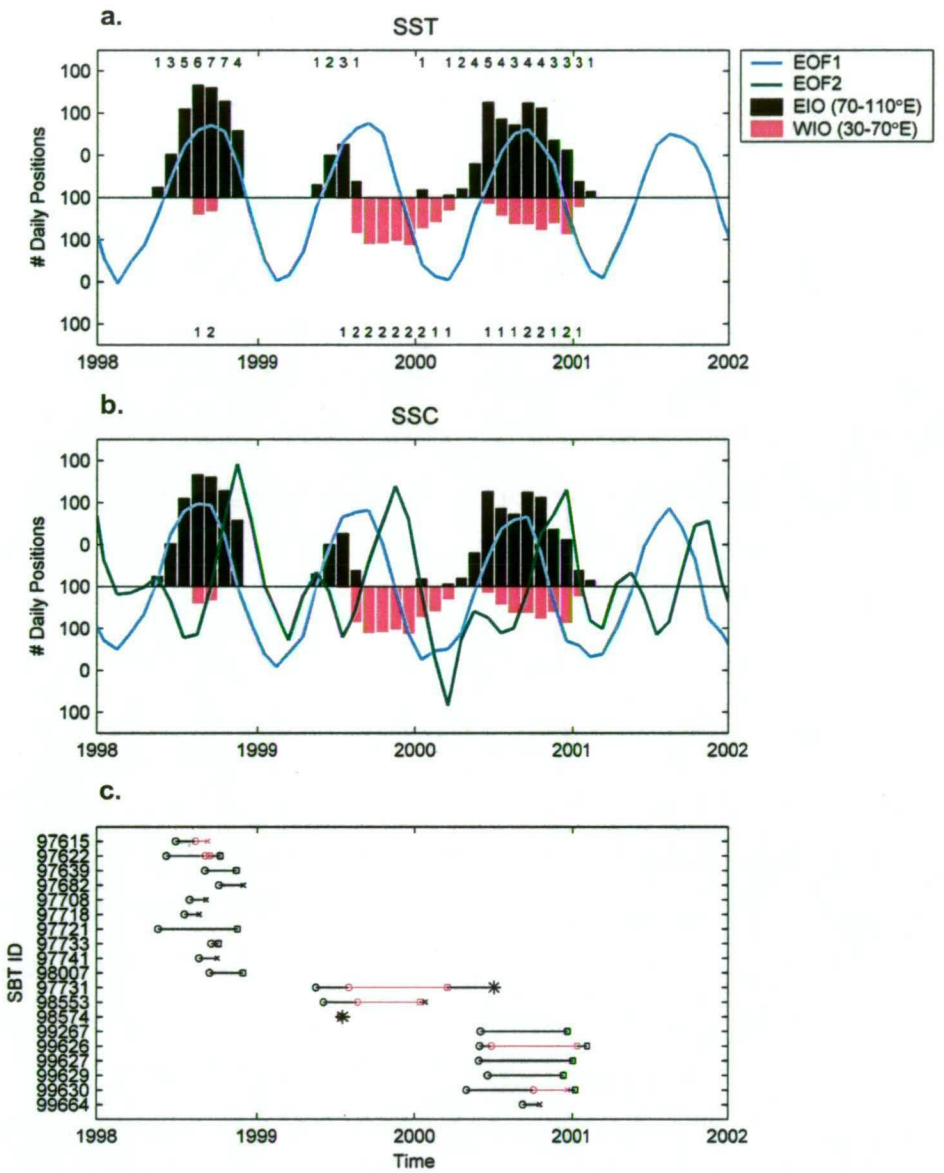

Fig. 2.4. SBT movements in relation to seasonal ocean processes. Juvenile SBT presence in the western (WIO, pink) and eastern (EIO, black) basin of the south Indian Ocean are overlaid by the (rescaled) principal component time-series of the dominant EOF mode(s) for (a) SST, and (b) SSC from Fig. 2.3. At the top (EIO) and bottom (WIO) of the panels are shown the number of fish represented per month. Panel (c) shows the arrival (o) and where available departure (□) times of individual fish, or else the event of premature recapture (*) or tag failure (x). The total number of fish (n) and number of daily geolocation positions (N) represented in the western basin are 1998: n = 2, N = 43; 1999: n = 2, N = 259; 2000: n = 4, N = 298; and in the eastern basin are 1998: n = 10, N = 617; 1999: n = 3, N = 147; 2000: n = 8, N = 716.

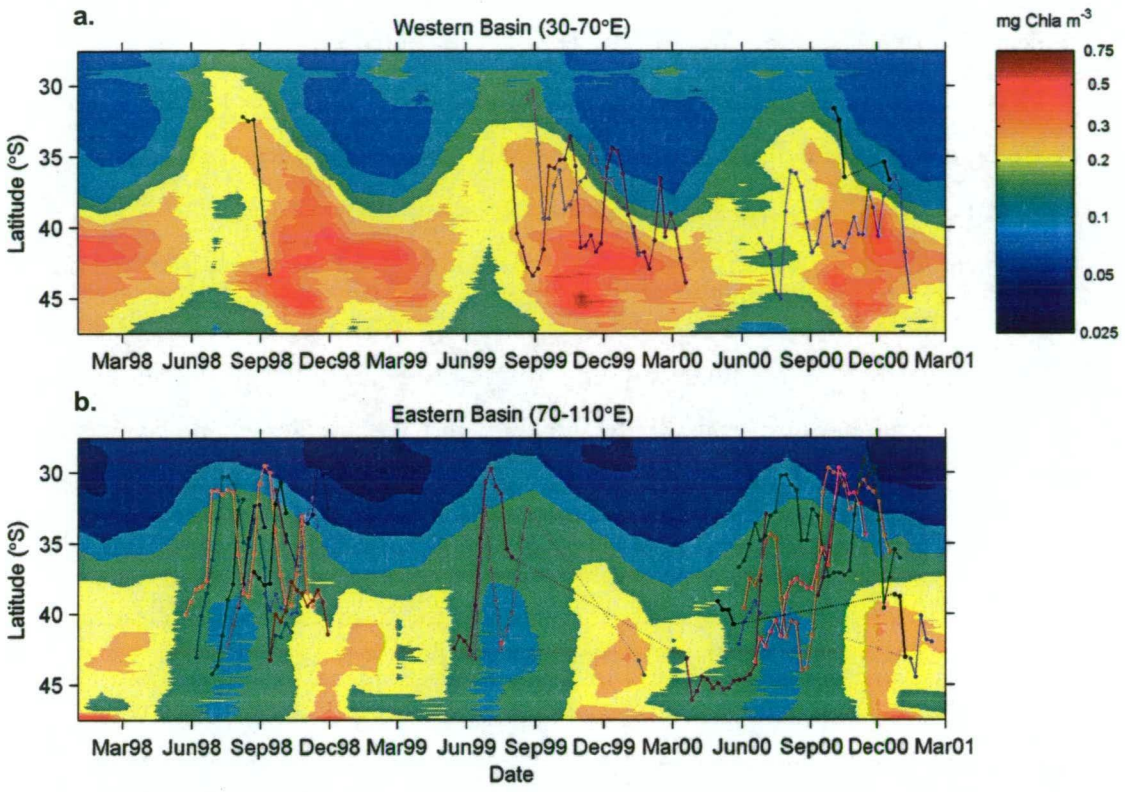

Fig. 2.5. Time-latitude diagrams of monthly SeaWiFS chlorophyll concentrations (mg m^{-3}) overlaid by average weekly positions of juvenile SBT carrying archival tags in the (a) western (n = 6) and (b) eastern (n = 19) basin of the south Indian Ocean. Colours indicate individual fishes. Dashed lines in panel (b) indicate periods when the individual moved into the western basin. However for SBT99630 (black line during 2000) relatively few positions were available (see Table 2.1).

Table 2.2. SBT behaviour within three oceanic regions of the south Indian Ocean. (1) Subtropical margin, (2) Mode-water formation region, and (3) Agulhas retroflection system. Core areas representative of each oceanic region are defined as shown in Fig. 2.8. Unless otherwise specified data are shown as mean (SD) across (n) fishes.

Oceanic region	Fish (n)	Days (% all data)	Days per fish	Mean daytime depth (m)	Maximum daytime depth (m)	Proportion daytime depth ≤50m	Proportion daytime depth ≥100m	ΔT/ΔZ surface 200m (°C)
(1) Subtropical margin	13	493 (24%)	38 (29)	53 (13)	216 (46)	0.64 (0.1)	0.16 (0.06)	3.45 (0.54)[a]
(2) Mode-water	18	616 (30%)	34 (24)	151 (53)	359 (74)	0.31 (0.18)	0.58 (0.18)	0.63 (0.52)[a]
(3) Agulhas retroflection	4	371 (18%)	93 (71)	114 (29)	318 (50)	0.42 (0.13)	0.43 (0.16)	2.71 (1.4)[b]

[a] Calculated for winter; [b] Calculated for spring

Four case-studies of individual SBT residencies illustrate why this may be the case. In the eastern basin, SBT resident in the subtropical margin region of relatively enhanced wintertime surface chlorophyll-a concentration tend to be epipelagic, predominantly occupying the surface layer of the water column (<50m, Figs 2.6a and 2.7a, Table 2.2). In comparison, south of 35°S in the colder, deeply-mixed waters of uniform temperature (11–13°C in the upper 300m) SBT spend the majority of daylight hours below 100m (Figs 2.6b and 2.7b, Table 2.2). Hence, whatever SBT are focussing on within the deeper layers of this mode-water region might not necessarily be expected to have any detectable surface expression. In this example, the individual is located directly south of the subtropical band of enhanced chlorophyll (Fig. 2.6b), so there is a possibility that the vertical movements of SBT (and/or their prey) might also have a horizontal component. However the temperature-depth profiles do not suggest this occurs unless SBT continue to target the cool water below the subtropical mixed-layer. Also shown are examples of a resident fish in the Agulhas retroflection system in the western basin located in the centre of the spring bloom (Fig. 2.6c), and one located on the northern boundary of a high chlorophyll zone extending south of 35°S (Fig. 2.6d). These examples respectively relate to the mid-spring positive phase of the SSC cycle identified in mode 2, and the early summer negative phase of the cycle identified in mode 1, of the EOF analysis. In both cases, there is a high component of mesoscale variability evident in the SSC, and the archival tag data show SBT utilizing areas with a wide range of surface (10–20°C) and subsurface (6–15°C) temperatures (Fig. 2.7c, d). Similar to the eastern basin cases, SBT dive patterns appear deeper in colder (SST < 15°C) water. However, dive patterns within the region of the Agulhas retroflection appear less predictable in general, with SBT spending a similar amount of time in shallow (<50m) and deep (>100m) sections of the water column (Table 2.2).

Notably, an individual fish may target primarily one, or more than one, of these oceanic regions. For example SBT98007 undertook a relatively late westerly migration, arriving in the south Indian Ocean in mid-September, and exclusively occupied mode water until late November when it undertook its return migration to arrive back in the GAB in early December (Table 2.1, Fig. 2.8c). In contrast, SBT97721 (Fig. 2.8b) moved a number of times between the mode water region (during most of June and August) and the subtropical margin (during most of July and September). Of the more westward migrants, SBT99626 (Fig. 2.8b) went directly to the Agulhas retroflection region, whereas SBT98553 (Fig. 2.8c) spent time along the way in both warm (May and August) and cold water (September) areas. Thus, there is variability both within and between individual fish with regard to patterns of movement and use of different areas during the annual southern Indian Ocean migrations.

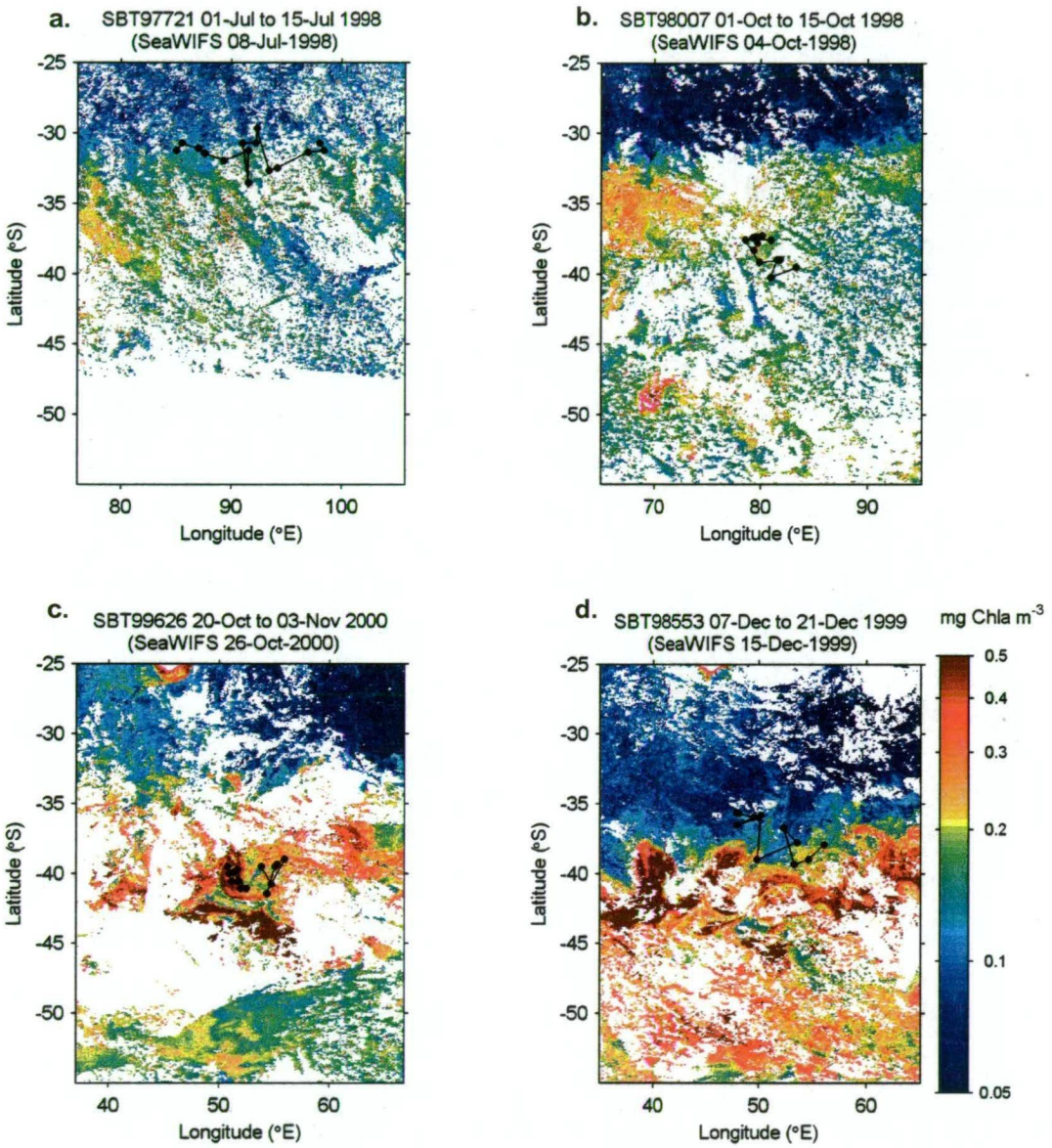

Fig. 2.6. Case-studies of SBT residency. Two-week snapshots from four individual fish: (a) sub-tropical margin (mid-winter), (b) mode-water region (early spring), (c) Agulhas retroflection system (cold front, late spring), and (d) Agulhas retroflection system (subtropical, late spring). Daily positions are estimated using a combination of light- and temperature-based geolocation (see Methods) and are overlaid on SeaWiFS weekly composite sea surface colour data.

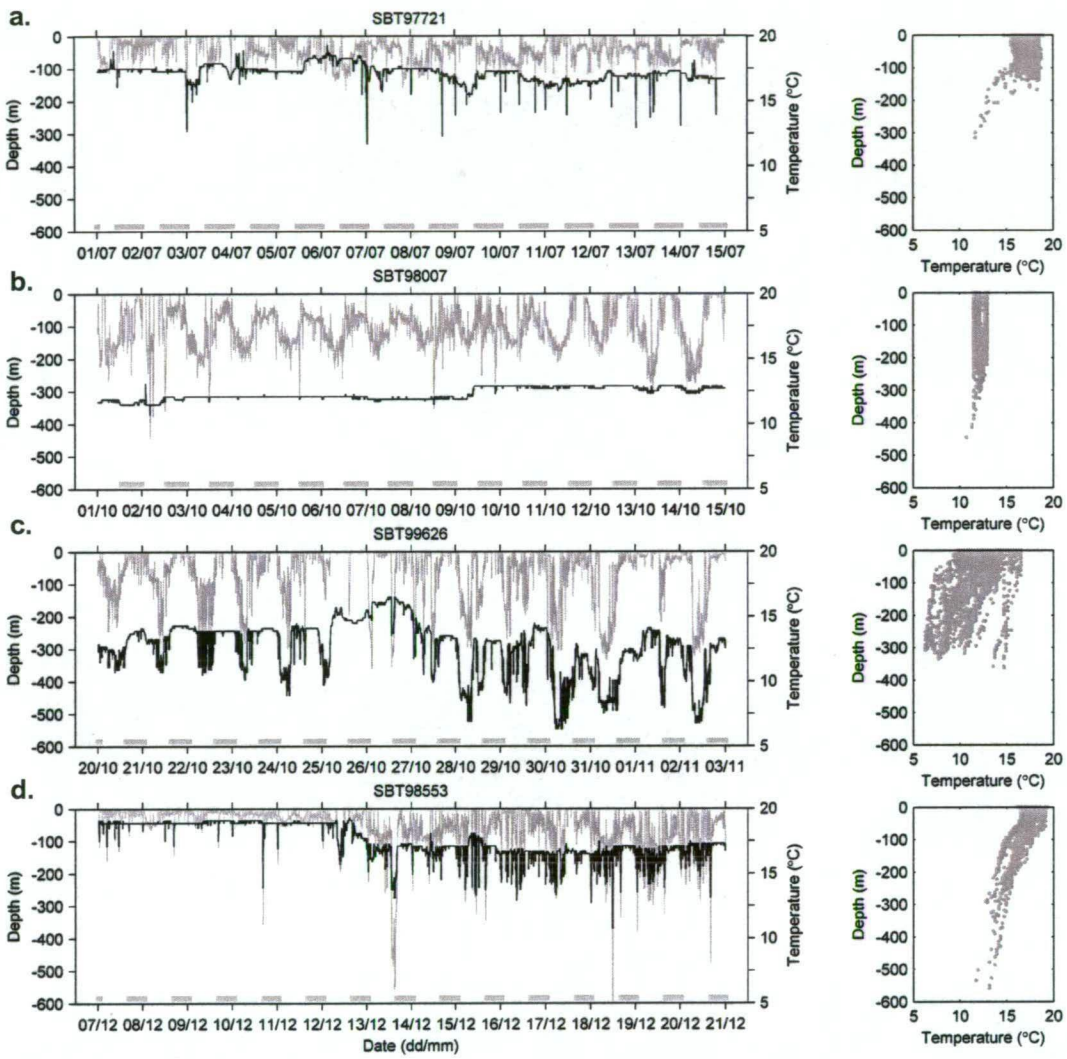

Fig. 2.7. Case-studies of SBT behaviour. Archival tag data (dive depth – grey, and water temperature – black) from the residencies of individual fish shown in Fig. 2.6. Shaded bars at the bottom of the panels indicate night time. Panels on the RHS show the temperature-at-depth profiles.

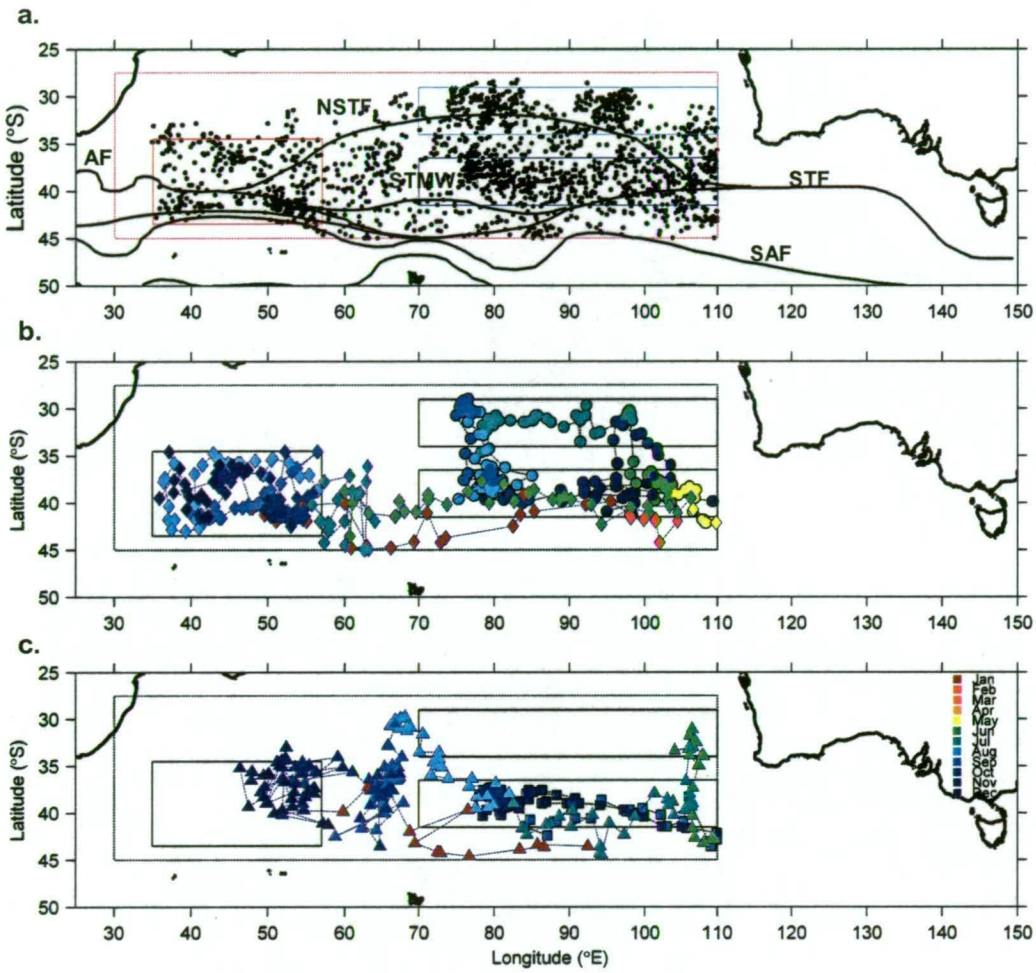

Fig. 2.8. Maps of SBT movements. (a) Location of all daily geolocation positions (N = 2179) from SBT (n = 19) within the study area (dashed box) and in relation to core areas representative of the (1) subtropical margin (cyan), (2) mode-water region (blue) and (3) Agulhas retroflection system (red)*. Panels (b) and (c) show individual migration tracks for SBT97721 (circles), SBT99626 (diamonds), SBT98007 (squares) and SBT98553 (triangles). Markers are coloured by month. Also shown for reference in panel (a) are the climatological positions (grey lines) of the major fronts of the area, where AF: Agulhas Front, STF: Subtropical Front, SAF: Subantractic Front, NSTF: North Subtropical Front, and also STMW: Subtropical Mode Water (Belkin & Gordon, 1996). *Note these are boxed for interpretive ease only: these are dynamic ocean features and are in fact more extensive than this.

DISCUSSION

We investigated whether juvenile SBT undertake their long-distance directed migrations to regions where environmental conditions are favourable for food production. Our analysis of remotely-sensed ocean temperature and ocean colour, in combination with tracking information from a large-scale tagging experiment, identified three primary oceanographic features in the south Indian Ocean, and their cycle of development and/or primary productivity, that may provide important seasonal feeding habitats for juvenile SBT. These are (1) the southern margin of the subtropical gyre, (2) the region of mode water formation in the central-eastern basin, and (3) the Agulhas retroflection system in the south-western basin. In two cases, the arrival of SBT coincides with seasonal maxima's in surface chlorophyll-a concentration indicating periods of high primary production and potentially high trophic transfer. However the ocean dynamics and biological processes operating in each of these three systems appear quite distinct. That SBT exploit such different systems, over such a vast spatial scale, suggests that this predator evolved this flexibility to achieve the resilience necessary to forage and survive in the vast and naturally heterogeneous temperate ocean environment.

Subtropical margin

The sea surface colour in the south Indian Ocean showed a strong seasonal pattern with a north-south contrast. This is consistent with previous studies focussed within the south-west Indian Ocean (primarily west of 70°E) based on satellite (Machu & Garcon 2001) and modelled (Machu *et al.* 2005) chlorophyll fields. These authors found that seasonal changes in light and nutrient availability were responsible for the observed phase opposition, and it is most likely similar mechanisms are at play throughout the basin. At the southern boundary of the oligotrophic subtropical gyre, primary production is limited by nutrient supply throughout most of the year, but in winter deeper stratification to ~100m, higher detritus remineralization and enhanced northward wind-driven Ekman advection of nutrients allow enhanced phytoplankton growth (Machu *et al.* 2005). However

in contrast, south of 35°S deeper wind-driven winter overturning (to >200m) removes phytoplankton from the euphotic zone and inhibits photosynthesis (Machu *et al.* 2005). Following winter, increased light availability combined with high levels of nutrients in the euphotic zone leads to strong primary production through the spring and summer in these southerly latitudes. Belkin & Gordon (1996) have also identified the southern boundary of the gyre as the North Subtropical Front, and suggested from its location in the region of wind convergence (between easterlies and westerlies, see Fig. 2.1) that it is largely a wind-driven feature.

The southern boundary of the subtropical gyre is not a previously documented "hotspot" for large pelagic predators. However, the oceanographic mechanisms and seasonal chlorophyll patterns documented here are analogous to the north-south movement of the Transition Zone Chlorophyll Front (TZCF) in the North Pacific, which is also driven by seasonal changes in light and nutrient availability (Polovina *et al.* 2001). This basin-scale feature is an important foraging and migratory corridor for albacore tuna and loggerhead turtles (Polovina *et al.* 2001). In the south Indian Ocean the subtropical margin is fished by the Taiwanese longline fleet, with high effort occurring from June to September *i.e.* mid-winter (Fonteneau 1997; Tuck, Polacheck & Bulman 2003). Although mainly targeting albacore tuna (*Thunnus alalunga*), juvenile SBT and other tunas are episodically targeted as well as caught as bycatch (Tuck *et al.* 2003). In addition, recent tracking studies have revealed other pelagic predators such as wandering albatross (*Diomedea exulans*, Weimerskirch & Wilson 2000) and subantarctic fur seals (*Arctocephalus tropicalis*, Beauplet *et al.* 2004) foraging along the subtropical margin in the south Indian Ocean during winter.

Mode water formation region

Within the eastern basin (>70°E), SBT spend extended periods in the region directly south of the subtropical margin (*i.e.* south of 35°S). These waters show no apparent seasonal enrichment in surface chlorophyll or frontal contrasts, and in fact show the lowest variability in surface chlorophyll of the entire basin (Fig. 2.2b). Bounded to the north by the subtropical margin and to the south by the

Subtropical Front and northern extension of the Antarctic Circumpolar Current, this region is additionally the most strongly affected by seasonal temperature and wind patterns, and has been identified as a source region of mode water, created by the process of deep vertical convection in the winter. Variously identified as a light type of Subantarctic Mode Water (McCartney 1982) or a Subtropical Mode Water (Belkin & Gordon 1996) it sinks and flows north under the lighter subtropical surface water as part of the general anticlockwise circulation of the subtropical gyre (McCartney 1982). The oceanic processes operating in the mode water formation region therefore have a signature observable in the EOF decomposition of the SST field, but have no SSC features.

In the mode water formation region temperature records from the archival tags show a homogeneous temperature of 11–13°C in the upper 300m of the water column. SBT within these waters are observed to target mesopelagic waters, largely between 100–300m but to greater depths in some individuals, and the strongly diel diving pattern suggests an association with the scattering layer (Gunn & Block 2001). While the diet of SBT in the south Indian Ocean has not been documented, unpublished SBT stomach contents data held by CSIRO indicates the predominant food item is ommastrophid squid (Gunn & Block 2001), which are known to make deep diurnal vertical migrations. Squid were also found to be an important prey item for juvenile SBT in the oceanic waters of the Tasman Sea, forming an increasing dietary component in the cooler subantarctic waters (Young *et al.* 1997). While the availability of squid specifically within the mode water formation region has not been documented, there is some evidence that mating/spawning in some squid species of the south Indian Ocean occurs during wintertime (Cherel & Weimerskirch 1999).

Agulhas retroflection system

In the south-western sector of the south Indian Ocean, the bottom topography exerts strong control over the eastward-flowing currents and the close juxtaposition of the Agulhas Front, the Subtropical Front and the Subantarctic Front creates intense mesoscale activity, and one of the most energetic and productive regions of the world oceans (Read *et al.* 2000). The Agulhas

retroflection system is a documented ocean "hotspot", supporting massive seasonal communities of land-based predators (*e.g.* seals, albatross and penguins) which breed on the Prince Edward and Crozet Islands during the spring and summer period (Pakhomov & Froneman 1999). This region has also long been heavily targeted by longline fleets targeting SBT (Fonteneau 1997; Tuck *et al.* 2003).

Within this region our analysis of surface chlorophyll showed the seasonal north-south contrast previously described, but additionally along the transition zone, in the vicinity of the Agulhas Front and extending east, was a distinct spring peak in surface chlorophyll. The timing of the arrival of juvenile SBT is strongly coincidental with this seasonal bloom both spatially and temporally. The proportion of juvenile SBT tagged in Australian waters which actually migrate this far is unclear; this study recorded 6 out of 19 fish (32%) moving into the western basin (<70°E, Table 2.1), but early failure of the tag (n = 4) or the light sensor (n = 1) plus one recapture early on the outbound journey leave the potential destination of 6 other migrant fish unknown. However, the relative cost-benefit ratio of these more extensive westward migrations has yet to be evaluated. It is worth noting that a one-way migration from the GAB directly to the centre (~90°E) of the subtropical margin or mode water regions, *i.e.* a distance of well over 3000km, takes a 3-year old SBT around 4 weeks at sustained swimming speeds of above 5km hr^{-1}. To reach 50°E in the Agulhas retroflection system requires around the same time again.

Seasonality of the temperate oceans

The migration of tunas has often been linked to oceanographic phenomena (Laurs & Lynn 1977). Recent studies have related tuna movement and distribution to environmental variability at all spatial and temporal scales, from local and mesoscale processes (Royer *et al.* 2004), to basin-scale seasonal (Polovina *et al.* 2001) and interannual ocean dynamics (Lehodey *et al.* 1997), and through to decadal scales of climatic variability (Ravier & Fromentin 2004). Environmental variability influences the distribution of ocean habitats, the level of primary production, community structure and transfer of energy to higher order predators.

The temperate seas, located midway between the tropics and the polar regions, are particularly changeable (Mann & Lazier 2005). Consequently, many marine fishes, mammals and seabirds undertake often extensive migrations to benefit from certain conditions at a particular time of year (Baker 1978). Timing migrations to coincide with seasonal patterns of production may confer a number of benefits; there is a high degree of predictability; the seasonal blooms in oceanic primary production occur over large spatial scales, hence within the temperate zone there can be a high degree of connectivity between different regions; and there is the likelihood of persistence of particular features. On the other hand, the distribution of primary production in the open ocean is still likely to be inherently patchy. For example, Llido *et al.* (2005) showed that the biological enhancement within the Agulhas retroflection system takes place as episodic localized phytoplankton bloom events, at two typical scales of 8–24 days and 40–60 days, which occur throughout the region in spring and summer; in this case rather than persistence of particular bloom events there is predictability of recurrence. Note that while spring peaks in meso-zooplankton biomass have been observed to coincide with phytoplankton peaks (implying rapid exploitation capability) (Limsakula *et al.* 2002), if the prey biomass lags production by some weeks (or months), tunas might also be expected to exploit the resultant biomass from specific bloom events at some time lag, or potentially in downstream areas.

The seasonal migrations of juvenile SBT are unusual in two ways. Most migratory species time their arrival in the temperate zone for the bloom of plankton growth that occurs in the spring, and are resident throughout the extended spring-summer-autumn period of enhanced production. Examples of these are the majority of albatross, penguin and seal species which breed on the subtropical and subantarctic oceanic islands of the south Indian Ocean (Pakhomov & Froneman 1999). In contrast, SBT can arrive in this ocean region in midwinter, and only their visits to the Agulhas retroflection system appear to fit clearly into this pattern. Many seasonal migrations consequently also follow a north-south pattern, presumably following this annual cycle of productivity; examples documented among the pelagic fishes include the poleward range expansions during feeding (*i.e.* non-spawning) migrations of bluefin tuna (*T. thynnus,* ABT)

in the North Atlantic (Block *et al.* 2001; Block *et al.* 2005); albacore (*T. alalunga*) in the North Pacific (Baker 1978; Watanabe *et al.* 2004); yellowfin (*T. albacares*) in the equatorial Atlantic (Maury *et al.* 2001) and also adult southern bluefin tuna in the southern oceans (Caton 1991). North-south seasonal movements alongshore, with some offshore component, also predominate for juvenile ABT (Stokesbury et al, 2004; Wilson et al, 2005; Block et al, 2005) and juvenile Pacific bluefin tuna (*T. orientalis*, PBT) (Kittagawa et al, 2000; Itoh et al, 2003; Block et al, 2003; Domeier et al, 2005). In contrast, while there is some north-south component the seasonal migrations of juvenile SBT from the coastal GAB to the oceanic South Indian occur on a much larger longitudinal than latitudinal scale, and remain entirely within the temperate latitudes (30–50°S) [3]. Therefore they are biologically dependent on the temperate seasonal cycles of production year-round.

In the South Indian Ocean very little is known about the winter foraging of most other top pelagic predators. Winter residency on the subtropical and subantarctic islands only occurs in the relatively few seabird and mammal species that have extended chick- or pup-rearing stages. For these central-place foragers, winter is commonly regarded as a period of increased foraging effort and range, and overall lower prey availability (Cherel, Ridoux & Rodhouse 1996a; Cherel & Weimerskirch 1999; Beauplet *et al.* 2004). However, winter is not reported as a period of lower prey availability for the wandering albatross, a species with extremely efficient locomotion and able to move continuously and rapidly over long distances to encounter isolated patches of prey (Cherel & Weimerskirch 1999; Weimerskirch, Gault & Cherel 2005). Among the pelagic fishes, the bluefin tunas are remarkable in possessing highly-evolved physiological adaptations for fast and efficient continuous swimming (Dickson 1995). In light of this, the spatial scale and persistence of the three seasonal ocean features identified in our

[3] Notably, while basin-scale migrations in the North Pacific have been documented in both juvenile albacore (Laurs & Lynn 1977; Polovina *et al.* 2003a) and juvenile PBT (Bayliff 1994;Itoh et al, 2003a), in both cases these appear to be one-way ontogenic migrations and return migrations occur once individuals are sexually mature. Furthermore, in PBT such extensive movements are known to occur in only a fraction of juveniles; however repeat trans-oceanic migrations have recently been recorded by a single individual (http://www.toppcensus.org), and low tag numbers mean the norm remains currently unknown.

analysis would provide a relatively high connectivity for a mobile predator able to move opportunistically. The variability evident in the movements between individual SBT further suggests that while these may be three key areas where the probability of good feed and/or habitat is relatively high, within each system resources are still likely to be patchily distributed in both space and time. Adopting a strategy as an efficient, wide-ranging and generalist predator may be the key to survival in this dynamic niche region between the southern edge of the oligotrophic subtropical gyre and the northern edge of the subantarctic circumpolar currents.

CONCLUSION

Our analysis showed the annual long-distance migrations of juvenile SBT places them within the south Indian Ocean during the period of maximum primary production along the southern margin of the subtropical gyre, and during the period of mode water production further south. Those individuals which undertake the more extensive migrations west to the dynamic Agulhas retroflection system arrive in time for the massive annual spring phytoplankton bloom events. In at least two of these oceanic environments, the enhanced primary production, coinciding with the presence of the tuna, potentially provides the basis for development of pelagic trophic webs and hence trophic transfer to higher order predators. However, less is known about the subsurface biological system within the mode water formation region. The dynamics of the three systems appear quite distinct, as does the extent to which each is known to be exploited by other pelagic species. Our findings illustrate the ability and flexibility of a top predator which has evolved to forage and survive in a vast and heterogeneous three-dimensional environment. Further demonstrated is how the multi-disciplinary approach integrating oceanographic and biological data can provide new insights into the motivations for movement and the specific timing and spatial extent of long-distance oceanic migrations. Developing an understanding of the ocean dynamics and pelagic ecosystems targeted by apex predators such as SBT is a fundamental first step if we are to begin making predictions under scenarios of human induced climate change and variability.

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APPENDIX A. EOF ANALYSIS

Briefly, given a set of N maps at times $t = 1...N$ containing data measurements at locations $m = 1...M$, an M x N data matrix F is constructed containing M rows (pixels m) and N columns (months t).

$$\mathrm{F} = \begin{bmatrix} F_{11} & F_{12} & \cdots & F_{1N} \\ F_{21} & F_{22} & \cdots & F_{2N} \\ \cdots & \cdots & \cdots & \cdots \\ F_{M1} & F_{M2} & \cdots & F_{MN} \end{bmatrix} \tag{1}$$

This matrix F can be written as the product of three matrices:

$$\mathrm{F} = \mathrm{U} * \Gamma * \mathrm{V}^{\mathrm{T}} \tag{2}$$

where the scalars on the diagonal of matrix Γ (M x N), called the singular values γ_k, are proportional to the eigenvalues λ_k (such that $\lambda_k = \gamma_k^2$) and explain the percentage of the variance of the field F that is accounted for by mode k

$$\%\ \text{Variance Mode k} = \frac{100 * \lambda_k}{\sum_{i=1}^{K} \lambda_i} \tag{3}$$

The columns of the matrix U (M x M) contain the eigenvectors *i.e.* the spatial EOF patterns associated with each singular value; and the columns of the matrix V^{T} (N x N) are proportional to the principal components time-series A such that

$$\mathrm{A} = \Gamma * \mathrm{V}^{\mathrm{T}} \tag{4}$$

$$\mathrm{A}^k(t) = \gamma_k \mathrm{V}^{\mathrm{T}k} \tag{5}$$

which gives the time evolution of the kth EOF. The field F can therefore be reconstructed by adding all K modes of the decomposition as:

$$F_m(t) = \sum_{k=1}^{K} \mathrm{U}_m^k \gamma_k \mathrm{V}^{\mathrm{T}k}(t) \tag{6}$$

3. Plasticity in vertical behaviour of migrating juvenile southern bluefin tuna in relation to oceanography of the south Indian Ocean

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Chapter 3

ABSTRACT

Electronic tagging provides unprecedented information on the habitat use and behaviour of highly migratory marine predators, but few analyses have developed quantitative links between animal behaviour and their oceanographic context. In this paper we use archival tagging data from juvenile southern bluefin tuna (*Thunnus maccoyii*, SBT) to (1) develop a novel approach characterising the oceanographic habitats used throughout an annual migration cycle on the basis of water column structure (*i.e.* temperature-at-depth data from tags), and (2) model how the vertical behaviour of SBT altered in relation to habitat type and other factors. Using this approach, we identified eight habitat types occupied by juvenile SBT between the southern margin of the subtropical gyre and the northern edge of the Subantarctic Front in the south Indian Ocean. Although a high degree of variability in behaviour was evident both within fish and between fish, mixed-effect models identified consistent behavioural responses to habitat, lunar phase, migration status and diel period. Our results indicate that SBT do not act to maintain preferred depth or temperature ranges, but rather show highly plastic behaviours in response to changes in the ocean environment. This behavioural plasticity is discussed in terms of the potential proximate causes (physiological, ecological) and with reference to the challenges posed for habitat-based standardisation of fishery data used in stock assessments.

Keywords: Southern bluefin tuna, archival tags, south Indian Ocean, seasonal migrations, habitat characterisation, pelagic habitat use.

Chapter 3

INTRODUCTION

Southern bluefin tuna (*Thunnus maccoyii*, SBT) have an almost circumpolar distribution throughout the temperate (30 to 50°S) Pacific, Atlantic and Indian Oceans, and are one of the world's most highly migratory fishes. Adult SBT undertake long-distance migrations from their temperate feeding grounds to a single known spawning region in the tropical Indian Ocean (Caton 1991). Juvenile SBT are also highly migratory, with those fish inhabiting the shelf waters of the Great Australia Bight in southern Australia during the austral summer known to disperse widely into oceanic waters (Caton 1991; Farley *et al.* 2007). An extensive archival tagging program has shown these movements are in fact regular, return migrations (Gunn *et al.* 1994; Gunn & Block 2001). While a proportion move eastward into the Tasman Sea, the majority undertake highly directed, long-distance migrations westward (up to 100 degrees of longitude *i.e.* some 8000 km) into the south Indian Ocean (CSIRO, *unpubl. data*; see methods).

The movements of tuna have often been linked to oceanographic phenomena (Laurs & Lynn 1977), and interactions between the distribution of top ocean predators and physical ocean features are increasingly being documented (Lehodey *et al.* 1997; Polovina *et al.* 2001). Recent approaches to modelling the spatial dynamics of a number of tuna species have predicted fish distribution on the basis of preferred oceanographic properties: usually temperature range, sometimes oxygen or salinity limits (Humston *et al.* 2000; Maury *et al.* 2001) and sometimes in combination with modelled prey fields (Bertignac, Lehoday & Hampton 1998; Kirby, Fiksen & Hart 2000). For example, in tropical tunas correlations have been found between large-scale east-west displacements of the western equatorial Pacific warm pool, predicted areas of high tuna forage and the distribution of commercial catches (Lehodey *et al.* 1998).

In comparison, the temperate bluefin tunas (northern and southern, *T. thynnus* and *T. maccoyii*) have unique physiological, biochemical and metabolic adaptations which enable them to exploit the widest range of oceanic habitats of all Scombridae (Block *et al.* 1998; Korsmeyer & Dewar 2001). These adaptations include large size, high metabolic rates, the ability to conserve metabolic heat and

elevate certain tissue temperatures above ambient, and fast and efficient continuous swimming enabling long-distance movements (Dickson 1995). The selection of different oceanic environments by these highly mobile pelagic predators, and their behaviour within those different habitats, is now observable with electronic tagging technologies (Gunn *et al.* 1994; Metcalfe & Arnold 1997). Archival tags can yield detailed long-term information on the movements and diving behaviour of individual fish, and their use of the pelagic habitat may then be interpreted directly within the oceanographic context.

During an annual migration juvenile SBT may encounter environments of widely varying physical characteristics. The near-surface circulation of the south Indian Ocean is relatively complex, dominated by a series of major circumpolar fronts separating a number of belts of water with quasi-uniform water mass properties (Belkin & Gordon 1996). Further, while bluefin species generally inhabit epi- to meso-pelagic waters, changes in the diving and surfacing patterns of individual fish have often been qualitatively reported in response to different water masses or changes in the vertical structure of the water column (Gunn & Block 2001; Itoh, Tsuji & Nitta 2003b; Stokesbury *et al.* 2004). However few studies have attempted to directly quantify relationships between vertical movements and environmental determinants (Kitagawa *et al.* 2000; Wilson *et al.* 2005). Improved understanding of the physical and biological factors influencing the vertical behaviour of commercial species is particularly receiving attention in light of the development of habitat-based stock assessments, which use information on fish behaviour to standardize fishery catch and effort statistics (Bigelow, Hampton & Miyabe 2002; Kleiber, Hinton & Uozumi 2003; Bigelow & Maunder 2007).

Analyses of biological data often include spatial (*e.g.* latitude, longitude) and temporal (*e.g.* seasonal) factors, not because they are thought to be important *per se*, but because they present a convenient proxy for examining biological and ecological processes, such as the seasonal movement of animals and changing habitats and habitat characteristics. In this study we take advantage of the uniquely detailed (and three dimensional) information on habitat that is provided by archival tags, and aim to quantify aspects of juvenile SBT vertical behaviour

directly in relation to oceanographic features of the south Indian Ocean. Specifically we (1) characterise the oceanographic habitats used during an annual cycle on the basis of water column structure (*i.e.* temperature-at-depth), (2) test whether and how the vertical behaviour patterns of SBT alter between different habitat types. In addition we test two other factors likely to influence vertical movement: lunar phase and migrating phase (*i.e.* whether fish behave differently when actively migrating). Our focus is to examine direct links between environment and behaviour, and particularly to evaluate the level of fish-to-fish variation. The observed habitat utilisation patterns are discussed with reference to the physiology and ecology of juvenile SBT, and also the implications for the interpretation of fishery catch and effort data.

METHODS

Archival tag data

The archival tag data used in this study form part of an extensive and ongoing program tagging juvenile SBT in the Great Australia Bight (Gunn & Block 2001). During the austral summers of 1998–2000 200 SBT were caught by pole-and-line and archival tags (model Mk7, Wildlife Computers, Redmond, WA) were surgically implanted into the peritoneal cavity ventral to the stomach (Gunn *et al.* 1994). The tags were set to Greenwich Mean Time and programmed to sample every 4 minutes the pressure, ambient light, and water and visceral temperatures. To date 51 (26%) tags have been recovered and data downloaded successfully from 47. Due to early recapture (n = 10), or early sensor (n = 4) or tag (n = 4) failure, long-term data (*i.e.* > 120 days) is available from 29 tags.

Daily longitudes were determined using proprietary light-based geolocation software (GeoControl v2.01.0002; Wildlife Computers, Redmond) relating the mid-point between sunrise and sunset to GMT (Hill 1994; Welch & Eveson 1999; Musyl *et al.* 2001). The accuracy of the longitudes were validated as far as possible by comparing the reported release and recapture locations with the nearest available position estimate (usually ± 2 days). The root-mean-square errors were 0.66° (n = 29) and 1.14° (n = 13) for release and recapture locations, respectively. These positions indicated that 19 fish (66%) moved west into the Indian Ocean (range = 35–148°E) during their first year at sea. To ensure the 1998 fish (n = 11) were not over-represented compared with the other release years (n = 3 in 1999; n = 5 in 2000), 6 randomly selected tags were included from this release bringing the total used in this analysis to 14 three year old fish (mean ± SD LCF = 99 ± 5 cm, range = 93–111 cm) (Eveson, Laslett & Polacheck 2004). Individual time-series spanned between 141 and 493 days (N = 4716 days total, Table 3.1).

Table 3.1. Individual release and recapture information for 14 tagged juvenile SBT which migrated westward during their first year at sea. Recapture locations include the Great Australia Bight (GAB), the Tasman Sea (TS), and the western, central, and eastern Indian Ocean (WIO, CIO and EIO respectively).

SBT tag ID	Release				Wild recapture					Time at liberty (days)	Complete tag data (days)	Zonal range (°E)
	Date	LCF (cm)	Latitude (°S)	Longitude (°E)	Date	LCF (cm)	Latitude (°S)	Longitude (°E)	Location			
97-682	03-Jan-98	93	-32.80	132.60	09-Jan-99	NA	-33.15	131.23	GAB	371	333 [F]	77–142
97-721	03-Jan-98	96	-32.80	132.60	15-Jan-99	114[C]	-33.35	131.82	GAB	377	339 [F]	75–140
97-615	26-Jan-98	100	-33.28	131.43	07-Jul-01	125	-39.62	28.52	WIO	1258	228 [F]	54–148
97-639	26-Jan-98	97	-33.12	132.00	05-Mar-03	153[C]	-33.43	131.75	GAB	1864	493 [L]	82–140
97-741	26-Jan-98	97	-33.30	131.62	29-Jul-00	121	-39.13	156.47	TS	915	283 [F]	78–143
98-007	26-Jan-98	96	-33.28	131.43	18-Feb-99	NA	-33.92	132.12	GAB	388	388 [R]	78–143
98-553	01-Mar-99	111	-33.30	131.48	18-Feb-01	133[C]	-33.88	132.52	GAB	720	330 [L]	46–135
98-574	01-Mar-99	102	-33.30	131.48	20-Jul-99	107	-39.75	103.68	EIO	140	141 [R]	104–134
97-731	01-Mar-99	95	-33.30	131.48	02-Jul-00	115	-32.50	80.52	CIO	489	490 [R]	35–138
99-267	17-Feb-00	100	-33.57	132.15	24-Jun-01	118	-39.80	154.67	TS	493	453 [TS]	76–136
99-626	17-Feb-00	99	-33.57	132.15	19-Jun-02	134	-32.30	87.50	CIO	853	370 [R]	36–134
99-627	17-Feb-00	103	-33.57	132.15	22-Jan-01	111[C]	-33.50	131.92	GAB	340	340 [R]	74–137
99-629	17-Feb-00	104	-33.57	132.15	09-Jan-02	NA	-33.58	132.32	GAB	692	265 [T]	69–139
99-664	17-Feb-00	99	-33.57	132.15	17-Nov-01	116	-40.92	37.18	WIO	639	263 [T]	79–144

[R, F, T, L] The data cease upon wild recapture (R), tag failure (F), light sensor failure (L) or external temperature sensor failure (T); except for SBT99-267 where data are not included beyond 15-May-01 when this fish crossed 148°E into the Tasman Sea (TS).

[C] Recapture length was reported after a period in Australian farm cages

There are well-documented difficulties in determining latitude from light-based geolocation (Hill & Braun 2001), and increasingly environmental data has been incorporated to improve position estimation, particularly satellite sea surface temperature (SST) data (Domeier *et al.* 2005). We similarly estimated latitude by comparing the surface water temperature recorded by the tag with satellite estimates. Briefly, using the Multi-Channel Sea Surface Temperatures (MCSST, night passes) 8-day 18 km interpolated product a longitude strip centred on the geolocation longitude (±1° E-W) was searched from 20–60°S. We display the median positions of all MCSST pixels matching within ± 0.2°C of the median temperature recorded by the tag in the surface 5 m during each 24 hr period. Using this method the latitudinal range containing 90% of all pixel matches is on average 1.06° and 0.84° to the north and south of the median respectively. The position estimates are used for mapping purposes only.

Habitat classification

To identify possible habitat groupings, clustering of the environmental data collected by the tags was conducted and cross-checked using a linear discriminant analysis (see also Field *et al.* 2001; Hinke *et al.* 2005b). To develop daily thermal profiles the tag temperature data for each 24-hour period were aggregated into (i) 5 m depth intervals from the surface to 10 m (ii) 10 m intervals from 10 to 100 m (iii) 25 m intervals from 100 to 200 m and (iv) 50 m intervals from 200 to 800 m. To provide a continuous profile a cubic smoothing spline was fit to the interval means; data outliers lying further than ± 2.5 standard deviations from the fitted curve were removed (n = 2.1% of raw data); and the curves re-fit. On 8.3% of dates the day and night data were sufficiently different (potentially due to considerable horizontal movement) to fit separate temperature-depth curves, and on 2.7% of dates the data were rejected because, for example, they were too aggregated within a restricted depth range or too variable to fit a plausible curve.

The thermal profiles (N = 4977) were then grouped using a hierarchical agglomerative clustering algorithm (AGNES) in R-software v1.9.1 package CLUSTER v1.9.6 (Kaufman & Rousseeuw 1990; Maechler *et al.* 2004). Each

fitted profile was treated as an observation, with each temperature per depth interval as a variable (Field *et al.* 2001). To take into account the unequal distribution of data between depth intervals, and prevent the procedure from being dominated by the near-surface observations, the data in each interval was scaled inversely to the number of profiles containing information at these depths (McCune & Grace 2002). Intervals below 550 m were not used as less than 10% of profiles contained data at these depths. The clustering algorithm was implemented on a dissimilarity matrix calculated from Euclidean distances using Wards linkage method (McCune & Grace 2002). This method tends to produce compact groups of well-distributed size, and preliminary investigations found it to be less sensitive to small outlier groups than other linkage methods, hence most useful for a basin-scale study.

To determine an appropriate number of habitat groups (k), both the agglomeration schedule (AS) and a linear discriminant analysis (LDA) were used to check the confidence of the grouping technique over a range of k values (McCune & Grace 2002). The LDA function was developed using half of the profiles randomly selected as a training set, and tested with the remainder, the procedure undertaken over 50 iterations for each value of k. At between 8–10 groups the LDA and AS each showed a plateau in both the Euclidean distance between merging groups and the misclassification rate (not shown); this indicates where high within-cluster coherency was obtained with minimal artificial splitting of similar groups. With reference to the existing literature on the major water bodies of the south Indian Ocean we selected 8 groups, at which on average the LDA predicted correctly in 81% of cases, indicating a relatively high reliability of the groupings.

Behavioural analysis

Four vertical behaviour parameters were modelled: (1) mean depth (m), (2) maximum depth (m), (3) the proportion of time spent in the surface 10 m, *i.e.* P(sfc), and (4) the proportion of time spent at depths below 100 m *i.e.* P(>100m). Log transformations were made to the depth parameters and an arcsin($\sqrt{P}$)

transformation to the probability parameters, to help stabilize the variance (determined by visual inspection of the residuals). All model results are reported back-transformed to the original units.

To examine the effect of oceanic habitat type and other factors on the vertical behaviour of SBT we used linear mixed effect models in R-software v1.9.1 package NLME v3.1-48 (Pinheiro & Bates 2000; Pinheiro *et al.* 2004). Mixed effect models take into account that there are multiple measurements on a single sampling unit (*i.e.* many observations per fish through time) and allow the within-individual errors to be correlated and/or have unequal variances. These are not modelled directly but as random effects. For any vertical behaviour parameter y_{ij}, where i denotes the fish and j the observation, within the habitat group H (determined by the classification procedure outlined above), the model then has the general form:

$$y_{ij} = H_{ij} + \zeta_i + \varepsilon_{ij} \quad (1)$$

where i denotes the fish and j the observation. This allows for two sources of error *i.e.* one associated with the variability among fish (ζ_i) and the other with the measurement process within fish (ε_{ij}). After examination of the autocorrelation function, the within-fish errors were specified to follow a 1st-order autoregressive process with an estimated autocorrelation value of ρ. Hence $\zeta_i \sim N(0, \sigma_\zeta^2)$ and $\varepsilon_{ij} \sim \rho\varepsilon_{ij-1} + \mu_{ij}$ where $\mu_{ij} \sim N(0, \sigma^2)$; *i.e.* ζ_i and μ_{ij} are both independent normal random variables. The resulting regression thus fits a random intercept to each individual rather than one for the population. The effect of fish-to-fish variability in response to habitat was further investigated by fitting a second model allowing random habitat effects, $h_{ij} \sim N(0, \sigma_{ih}^2)$, for each fish. A likelihood ratio (LR) statistic based on the restricted maximum likelihood (REML) was used to test between the random-effects structure of the two model forms (Venables & Ripley 2002).

Finally, we investigated the influence of two other factors widely expected to influence fish vertical behaviour: (1) lunar phase (visible fraction of the disc, a continuous variable where 0 is the dark moon and 1 is the full moon); and (2) whether the fish was actively migrating or not (a binary 0–1 indicator variable).

Migration was determined visually from the light-based geolocation longitude time-series of individual fish (with reference to SST-based latitudes where necessary) and required a minimum of 5 consecutive days of directed movement. Data recorded outside the GAB averaged 217 ± 98 days (range = 24–403) per fish, of which the average number of migration days was 59 ± 25 (range = 24–102) per fish. For any vertical behaviour parameter y_{ij} the model then has the general form:

$$y_{ij} = H_{ij} + M_{ij} + \beta L_j + \zeta_i + \varepsilon_{ij} \quad (2)$$

where M_{ij} is the migration effect for fish i at time j, L_j is the lunar phase at time j and β is the regression coefficient for L. The addition of these two terms to model (1) as fixed effects, plus their interaction terms with habitat (H_{ij}), was done as a stepwise procedure and tested using LR based on maximum likelihood (ML) (Venables & Ripley 2002). All P-values reported for terms within the models are based on Wald F-tests.

Confidence intervals (2.5% and 97.5% quantiles) were calculated for the model predictions based both on fixed effects alone (which corresponds to the best prediction "averaged" over fish – useful for predicting for the "population"), and incorporating ±1.96 SD of the random effect (which, assuming the model coefficients are known exactly, incorporates the fish-to-fish variability and may be interpreted as the predictions for a "random" fish sampled from the "population"). Note these are non-symmetrical about the back-transformed values.

A full model which contained all the fixed effects in model (2) above plus their interactions was initially fitted to the full data series for each behavioural parameter, with Day-Night as an additional factor. These showed a significant effect of Day-Night (DN) as a factor influencing all four behavioural parameters, plus a significant DN:lunar and DN:habitat interaction in three and four of the behaviour models respectively indicating these terms influenced day and night behaviour differently. Therefore, all the models described above were fitted separately to the day and the night data.

RESULTS

The 14 tagged SBT remained largely within southern Australian waters throughout the summer season, moving out of the GAB to the south-east in late summer or autumn, and a number spent time in the waters west of Tasmania (140–148°E) before beginning their migration west (Fig. 3.1). The migration schedule was variable between individuals, with rapid movements westward beginning as early as April in some fish, and as late as August in others. These periods of rapid migration were largely observed in the eastern basin (east of 70°E), although notably four individuals continued as far west as the areas of strong eddy activity in the Agulhas region in the south-western basin (west of 70°E, Table 3.1). During winter and spring SBT were distributed widely throughout the south Indian Ocean between 30–45°S. Return migrations were initiated either in the spring (October-November) for an early summer return to the GAB, or in early summer (December-January) for a mid-summer return.

Oceanic habitats

The cluster analysis revealed juvenile SBT use eight major oceanic habitat groups across the south Indian Ocean (Figs 3.1 and 3.2). Although derived solely from tag-based temperature/depth profiles, these groupings were in general spatially cohesive and correspond well with existing descriptions of the upper ocean circulation in the literature (McCartney 1982; Nagata *et al.* 1988; Belkin & Gordon 1996; James *et al.* 2002; Kostianoy *et al.* 2004; Yuan *et al.* 2004). During an annual migration cycle most SBT sampled all oceanic habitats (excluding HAB8, see below). However, individuals showed variation in the amount of time spent in each (Table 3.2). By way of illustration, the full time-series of temperature-at-depth profiles for three SBT, released in 1998, 1999 and 2000 respectively, together with the habitat classifications, are shown in Fig. 3.3.

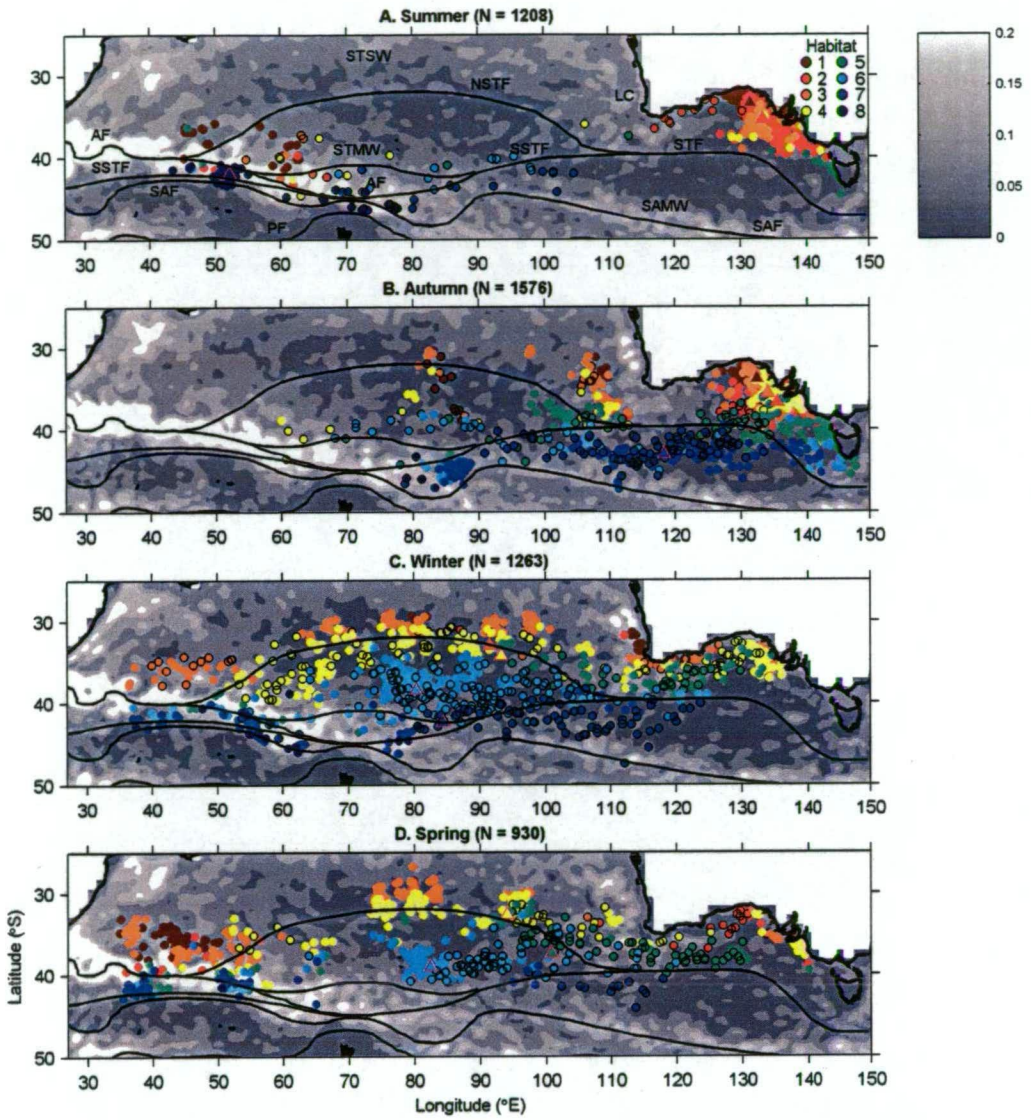

Fig. 3.1. Daily positions (N = 4716) for 14 SBT shown by season and habitat. Habitat groups 1–8 (see Fig. 3.2) are indicated by colour. Black circles indicate periods of active migration. Overlaid is the mean frontal pattern of the south Indian Ocean adapted from Belkin and Gordon (1996). Notation: LC – Leeuwin Current; STSW – Subtropical surface water; STF – Subtropical front, and its north (NSTF) and south (SSTF) components; AF – Agulhas front; SAF – Subantarctic front; PF – Polar front; STMW – Subtropical Mode Water; SAMW – Subantarctic Mode Water. Background shows the standard deviation (m) of the seasonal mean mapped sea level anomaly (MSLA), indicating areas of high mesoscale activity (white). MSLA obtained from the 10-day SSALTO/DUACS NRT product over 1 January 1998 to 15 May 2001 (http://www.jason.oceanobs.com). Austral seasons as per the World Ocean Atlas 1998 (WOA98) are: Summer (Jan-Mar), Autumn (Apr-Jun), Winter (Jul-Sep), Spring (Oct-Dec). Triangles give the median seasonal habitat location, for the seasons accounting for the majority (>70%) of profiles in a habitat (for Fig. 3.2).

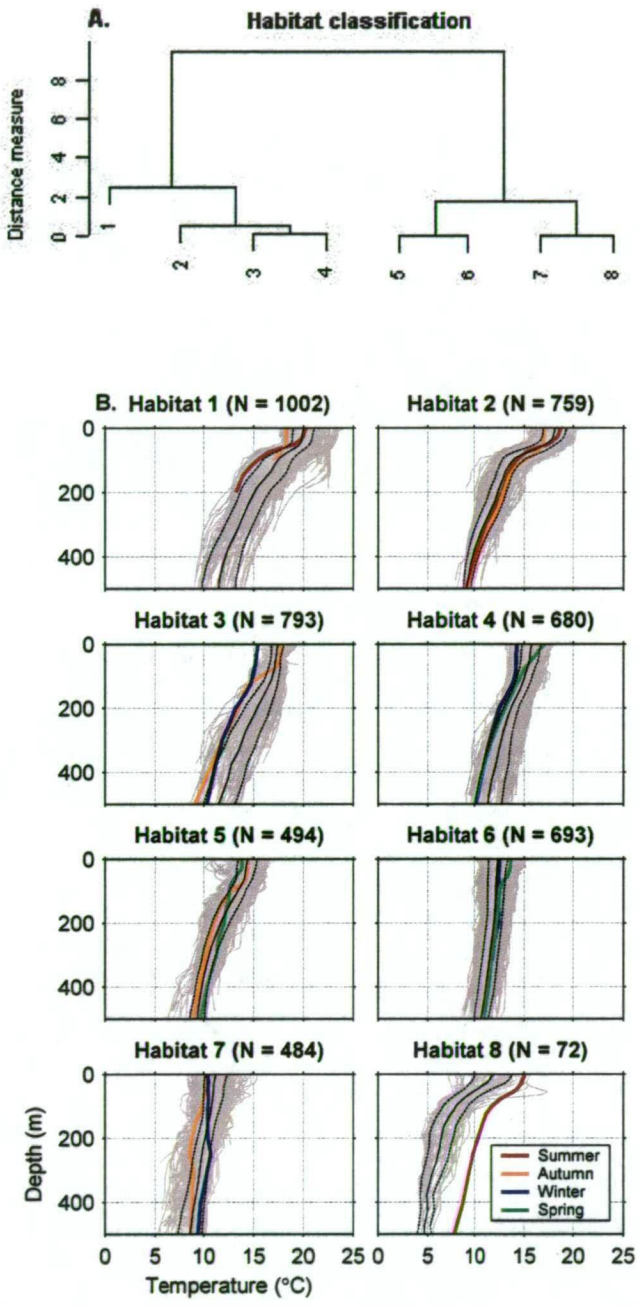

Fig. 3.2. Habitat grouping based on clustering (see Methods) of daily thermal profiles. (a) Cluster dendogram showing group relationships (b) Vertical temperature profiles (grey) of the eight major habitat groups (mean ± SD in black) together with the WOA98 seasonal climatological temperature profiles for the seasonal median habitat locations (see Fig. 3.1).

Table 3.2. Total number of days (maximum number of consecutive days) spent in occupancy of eight major oceanic habitats by individual juvenile SBT.

SBT	Habitat							
	HAB1	HAB2	HAB3	HAB4	HAB5	HAB6	HAB7	HAB8
97-682	59 (21.5)	50.5 (15)	74.5 (11.5)	48.5 (7)	54 (22.5)	17 (2.5)	26.5 (15)	0
97-721	20 (11)	100 (31)	45.5 (12.5)	29 (6.5)	50.5 (23)	77 (29.5)	16 (6)	0
97-615	28 (17)	45 (7.5)	13 (7)	35.5 (12.5)	53.5 (11)	26.5 (17)	15.5 (14)	0
97-639	166 (106.5)	101.5 (71)	70 (18)	79 (8)	22.5 (11)	48.5 (41)	2 (2)	0
97-741	45.5 (12)	78 (17)	49 (7)	52.5 (13)	14.5 (4)	36.5 (18)	3 (2)	0
98-007	25 (6)	141.5 (54)	61 (35)	49 (22)	23.5 (7)	63 (57)	25 (12)	0
98-553	37.5 (26)	13 (5)	72 (24.5)	67 (19)	13 (3)	50 (13)	65.5 (53)	0.5 (0.5)
98-574	86.5 (80)	2 (1)	22.5 (11)	3 (3)	4 (2)	1 (1)	20 (12)	0
97-731	110 (29.5)	27.5 (4)	63.5 (34)	30.5 (3.5)	27.5 (5.5)	71 (14)	89.5 (12)	40.5 (21.5)
99-267	103 (33.5)	59 (8)	54 (25)	64 (15.5)	59 (8)	28.5 (9)	60.5 (26)	2 (1)
99-626	77.5 (33)	15.5 (3)	38.5 (17)	30.5 (6)	36.5 (6)	53.5 (7)	64.5 (17)	9.5 (1.5)
99-627	58.5 (27)	32.5 (6)	73 (19.5)	52.5 (15)	34.5 (9)	65 (42.5)	8 (8)	0
99-629	66.5 (61)	14 (6)	23.5 (14)	32.5 (22)	14 (5)	82.5 (57)	21.5 (15.5)	0.5 (0.5)
99-664	67 (29)	25 (4)	80.5 (12)	39 (12)	7.5 (3)	17 (11)	4 (2)	0
Mean ± SD	68 ± 40 (35 ± 28)	50 ± 41 (17 ± 21)	53 ± 22 (18 ± 9)	44 ± 19 (12 ± 6)	30 ± 19 (9 ± 7)	46 ± 25 (23 ± 19)	30 ± 28 (14 ± 13)	4 ± 11 (5 ± 9)

Habitat 1 (HAB1) largely represented the GAB during the summer and autumn, with 78% of these profiles located within the area 126–136°E, 30–36°S (Figs 3.1a and 3.2b). These waters were characterized by a very warm surface layer (17–22°C) and a shallow thermocline around 60–80 m. Located primarily in shelf waters further to the south-east, HAB2 (Fig. 3.2b) also had relatively warm (17–19°C) surface waters but a stronger and shallower thermocline near 50 m. Both groups, but particularly HAB1, also included a small number of similar profiles recorded during late spring and summer in the far western Indian Ocean in the Agulhas region (Fig. 3.1a, d). Generally HAB1 and HAB2 profiles recorded in the east tended to be cooler than those recorded in the west, consistent with hydrographic observations (Belkin & Gordon 1996).

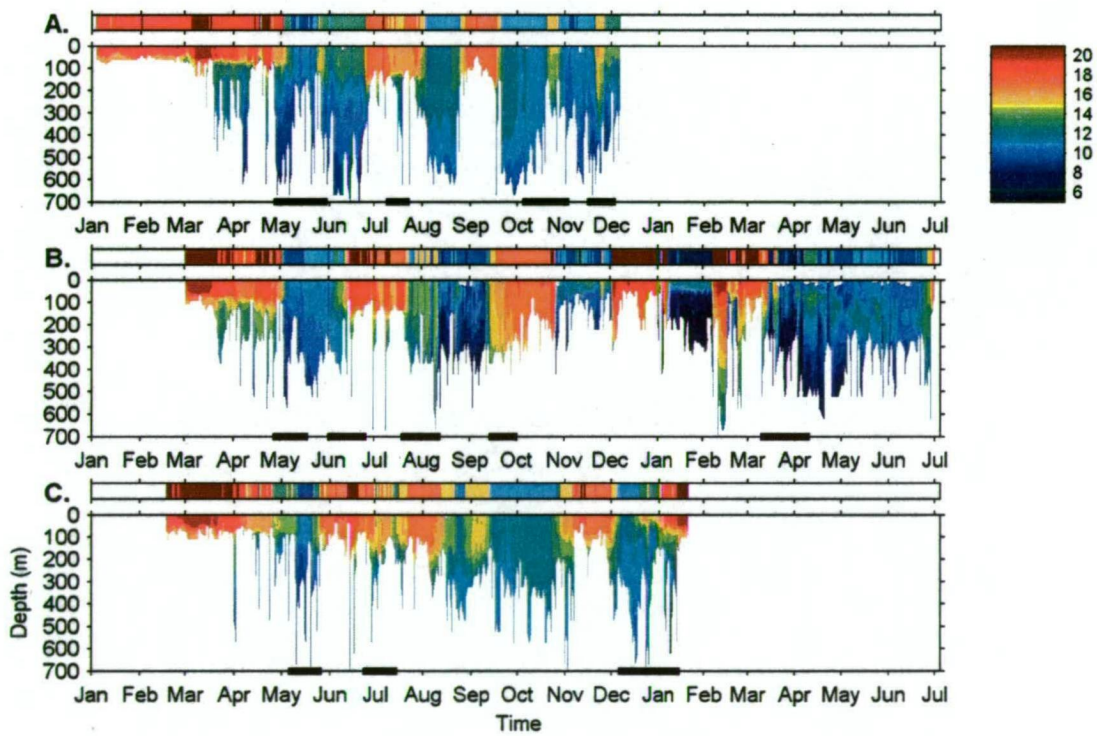

Fig. 3.3. Contoured temperature (°C) at depth (m) time-series from three individual SBT (a) 97-721, (b) 97-731 and (c) 99-627, tagged and released in 1998, 1999 and 2000 respectively. Scale indicates water temperature (°C). The habitat grouping is shown in the bar above each panel (coloured as in Fig. 3.1). Black bars indicate periods of active migration. Note the summer residency of SBT 97-731 in HAB8 during December-January 2000.

HAB3 and HAB4 largely represented the subtropical waters along the southern margin of the subtropical gyre, an area widely utilised by SBT during winter/spring (Fig. 3.1c, d; Table 3.2). This margin has been termed the North Subtropical Front (Belkin & Gordon 1996) and the two habitats, separated latitudinally across the basin, appear to lie to the north and south of this feature respectively. These waters were characterized by surface temperatures around 15–18°C and an eroded thermocline deepened to 100–150 m (Fig. 3.2b).

HAB5 consisted of profiles primarily recorded east of 90E throughout autumn to spring. This habitat had surface temperatures between 13–16°C and a deepened autumn-winter thermocline near 150 m (Fig. 3.2b), and in general was located to the north of the Subtropical Front. Located at similar latitudes to HAB5 in the central basin (70–100°E), HAB6 was a habitat used by SBT mainly during winter and spring (Fig. 3.1c, d). These profiles showed uniform waters of 11–14°C mixed deeply to below 400 m (Fig. 3.2b), a distinct homogeneous structure known as Subtropical Mode Water (McCartney 1982; Belkin & Gordon 1996).

HAB7 and HAB8 represented the coldest waters inhabited by these juvenile SBT, and were recorded in the southern-most latitudes. HAB7 was a complex group of profiles which included deeply mixed waters, profiles with a thermocline near 100 m, and a substantial number with temperature inversions (Fig. 3.2b). It seems reasonable to suggest that this group contained a mixture of waters between the southern edge of the Subtropical Front and the northern edge of the Subantarctic Front, including Subantarctic Mode Water. Finally, HAB8 was comprised of a small number of very cold profiles with surface waters near 12°C and a sharp thermocline in the upper 100m to 7°C, declining to 5°C at 400 m (Fig. 3.2b). These profiles were recorded in the dynamic frontal region in the south-western basin where there is a triple confluence of the Agulhas Front/South Subtropical Front/Subantarctic Front (Fig. 3.1). The HAB8 profiles come from only two fish, primarily from one during the summer following release (*i.e.* during January-February as a four year old, Fig. 3.3b), and given the small amount of data available HAB8 was not included in the behavioural analysis.

Vertical behaviour models

The mixed-effect models indicated that mean depth, maximum depth, the proportion of time spent in the surface 10 m, *i.e.* P(sfc), and at depths below 100 m, *i.e.* P(>100m), were all significantly correlated with habitat type during both the day and the night (model (1), Table 3.3). In general, in the cooler habitats the mean depth, maximum depth and P(>100m) was greater, while P(sfc) was greater during the night and reduced during the day (Fig. 3.4). Taking into account the variability associated with both the fixed effects (dashed line, interpreted as predictions for an "average fish"), and the random fish effect (dotted line, interpreted as predictions for a "random fish"), significant differences between the day and night periods were predicted for the two coldest habitats (HAB6 and HAB7) in all behavioural parameters except maximum depth (Table 3.3, Fig. 3.4).

Table 3.3. Predicted values (95% CI based on the fixed effects) for four vertical behaviour parameters based on habitat (model (1)).

		Behavioural parameter			
Habitat[b]	Period[a]	Mean depth (m)	Max. depth (m)	P(surface)	P(>100m)
1	Day	30 (25–35)	116 (103–130)	0.32 (0.28–0.37)	0.08 (0.05–0.11)
	Night	32 (29–35)	124 (117–133)	0.25 (0.22–0.29)	0.03 (0.02–0.04)
2	Day	34 (30–40)	143 (127–160)	0.29 (0.25–0.34)	0.10 (0.06–0.13)
	Night	26 (24–29)	133 (124–142)	0.32 (0.28–0.35)	0.03 (0.02–0.04)
3	Day	34 (29–40)	136 (122–153)	0.29 (0.25–0.33)	0.09 (0.06–0.13)
	Night	29 (26–32)	137 (128–147)	0.30 (0.27–0.34)	0.04 (0.03–0.05)
4	Day	44 (38–52)	185 (165–207)	0.24 (0.20–0.28)	0.15 (0.11–0.19)
	Night	30 (27–33)	173 (162–186)	0.38 (0.34–0.42)	0.06 (0.04–0.07)
5	Day	58 (49–68)	242 (214–274)	0.20 (0.16–0.24)	0.23 (0.18–0.28)
	Night	29 (26–33)	199 (185–215)	0.41 (0.37–0.46)	0.07 (0.05–0.08)
6	Day	81 (69–96)	266 (235–299)	0.09 (0.06–0.12)	0.38 (0.32–0.44)
	Night	37 (33–41)	209 (195–225)	0.36 (0.31–0.40)	0.12 (0.10–0.14)
7	Day	115 (97–137)	307 (270–349)	0.05 (0.03–0.08)	0.58 (0.51–0.65)
	Night	35 (31–40)	220 (202–239)	0.39 (0.34–0.44)	0.13 (0.11–0.16)

[a] All mixed-effect models were fitted separately to the day-time and night-time data.
[b] Based on a Wald test all models showed a highly significant habitat effect ($P < 0.0001$).

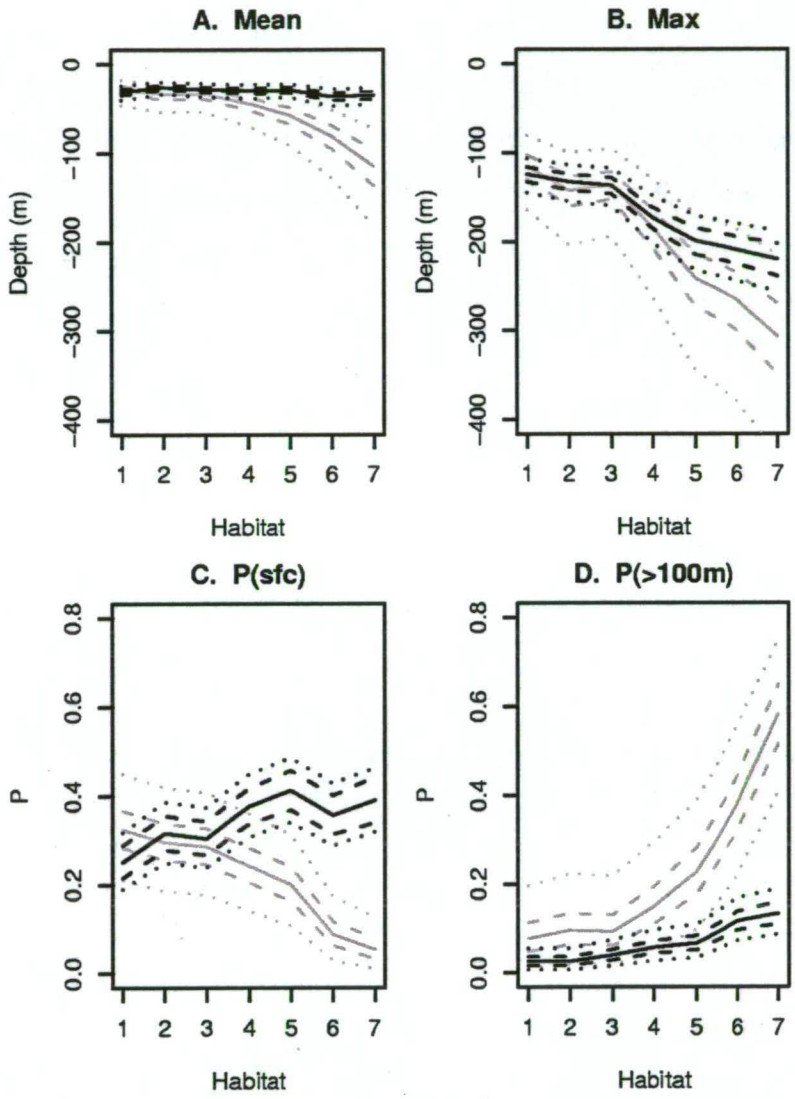

Fig. 3.4. Results of mixed-effect models predicting habitat effects on four behavioural parameters (a) mean depth (m), (b) maximum depth (m), (c) proportion of time spent in the surface 10 m, P(sfc), and (d) proportion of time spent below 100 m, P(>100m). Models were fitted separately to day-time (grey) and night-time (black) data. Shown are the estimated parameter (solid line), and the 95% confidence intervals based on the fixed (dashed) and random (dotted) effects (see Methods). Note that although habitats are actually discrete factors, line plots are used to aid interpretation.

For all modelled day-time behaviours a significant improvement in model fit occurred by including habitat as a random effect, indicating significant variability existed between the responses of individual fish to habitat type (LR tests, Table 3.4). Night-time behaviours were more consistent between fish, with only maximum depth showing significant variability between individuals. However, the results from these models were similar overall to the previous models, with the predictions for individual fishes generally lying within or close to the confidence intervals previously developed for the "random fish" (Fig. 3.5).

Table 3.4. Results of testing for fish-to-fish variability in behavioural responses to habitat.

	Day		Night	
	Likelihood ratio [a]	*P*-value	Likelihood ratio	*P*-value
Mean	52.27	0.0025	35.79	ns
Max	71.91	<0.0001	81.38	<0.0001
P(Sfc)	51.91	0.0027	9.65	ns
P(>100m)	90.92	<0.0001	41.18	ns

[a] Likelihood ratio statistic and associated *P*-value are shown for comparison of mixed-models including habitat as both a fixed and random effect against models including habitat as a fixed effect only; ns indicates no significant difference ($P > 0.01$). Degrees of freedom for each model are 37 and 10 respectively.

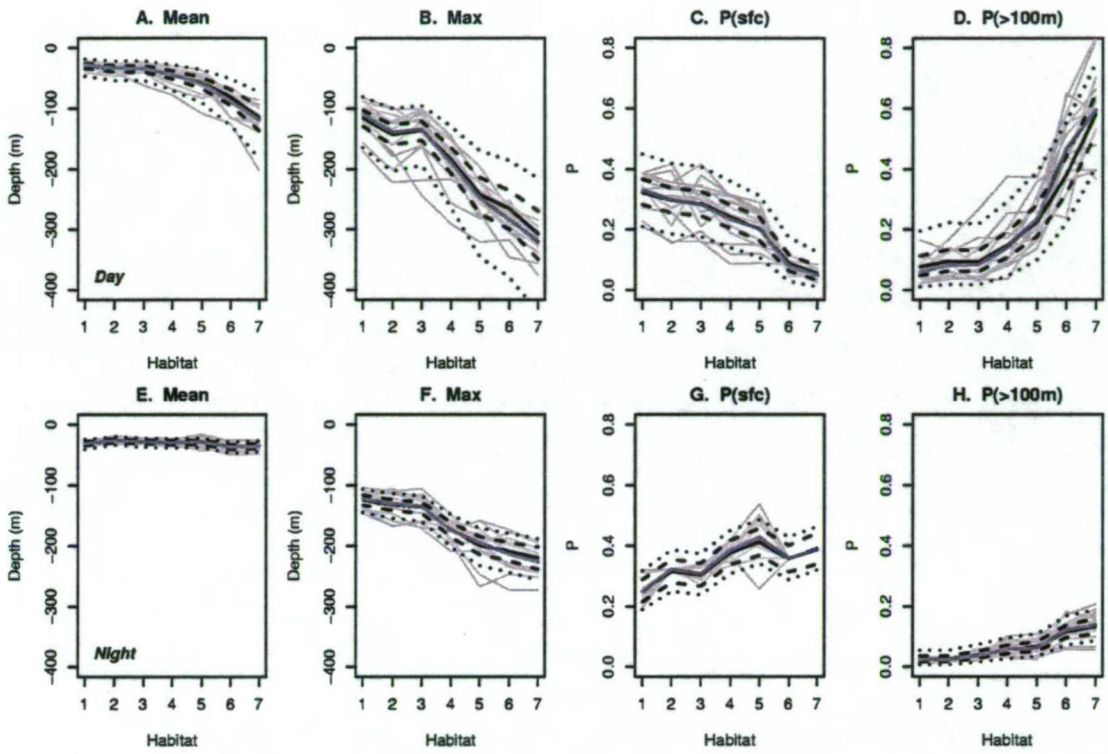

Fig. 3.5. Results of mixed-effect models including habitat as both a fixed and random effect. Overall model predictions (grey, bold) and predictions for individual fishes (grey) are shown, overlaid on the predictions (black) from the model including habitat as only a fixed effect (see Fig. 4). Day-time and night-time models are shown in the upper (a-d) and lower (e-h) panels, respectively. Model significance values are shown in Table 3.4.

The effect of the two other factors tested, lunar phase (continuous variable) and migrating status (binary 0–1 variable), was variable between day and night periods. Three of the four day-time behavioural parameters showed a significant effect of migrating status (mean: LR = 10.02, $P = 0.0015$; max: LR = 21.71, $P < 0.0001$; P(sfc): LR = 0.008, $P = 0.93$; P(>100m): LR = 13.96, $P = 0.0002$) and in all four cases the best model fit was obtained with a habitat:migration interaction *i.e.* allowing the migration effect to vary across habitats (mean: LR = 46.61, $P < 0.0001$; max: LR = 37.6, $P < 0.0001$; P(sfc): LR = 32.52, $P < 0.0001$; P(>100m): LR = 25.45, $P = 0.0003$). Migrating fish in HAB1–5 were predicted to spend significantly more time below 100 m, and

within the warmer habitats to generally occupy deeper depths and spend reduced time at the surface although the patterns varied across behavioural parameters (Fig. 3.6a-d). There was no significant lunar effect or habitat:lunar interaction detected for any day-time behaviour ($P > 0.2$ in all models). The results of the Wald tests on each variable in the final best-fit models are shown in Table 3.5.

There was a strong influence of lunar phase on all night-time behavioural parameters (Fig. 3.6e-h) except maximum depth (mean: LR = 242.7, $P < 0.0001$; max: LR = 3.39, $P = 0.066$; P(sfc): LR = 356.3, $P < 0.0001$; P(>100m): LR = 19.9, $P < 0.0001$). Mean depth was predicted to deepen, P(sfc) to be strongly reduced and P(>100m) to marginally increase on a full moon, and vice versa on a dark moon. Migration status influenced only maximum depth and P(>100m) (mean: LR = 3.08, $P = 0.08$; max: LR = 29.4, $P < 0.0001$; P(sfc): LR = 2.55, $P = 0.11$; P(>100m): LR = 20.8, $P < 0.0001$), with a predicted increase in both parameters for migrating fish. Therefore, at night-time P(>100m) was the only behavioural parameter influenced by both migration status and lunar phase, although the combined effect of both factors resulted only in a small increase in P(>100m). For all behavioural parameters the lunar and/or migration effects on night-time behaviour were predicted to be consistent across habitats (*i.e.* the habitat:lunar interactions and habitat:migration interactions were non-significant, $P > 0.04$ in all cases). For example, during the full moon (relative to the dark moon) mean depth at night was predicted to deepen by a factor of 2.27 (CI = 2.07–2.5) across habitats, and during migration (relative to non-migrating) maximum depth at night was predicted to increase by a factor of 1.21 (CI = 1.13–1.29) across habitats.

The strong influence of lunar phase on three of the four night-time behavioural parameters meant persistent diel differences, *i.e.* no overlap in predicted day (Fig. 3.6a-d) and night (Fig. 3.6e-h) ranges regardless of moon phase or migration status, were only predicted in all three for the coldest habitat. In HAB7 mean depth was predicted to be shallower, P(sfc) higher and P(>100m) lower during the night-time as compared with the day-time for all phases of the

moon and all migration phases. P(>100m) was also always significantly lower in HAB6 during the night-time as compared with the day-time.

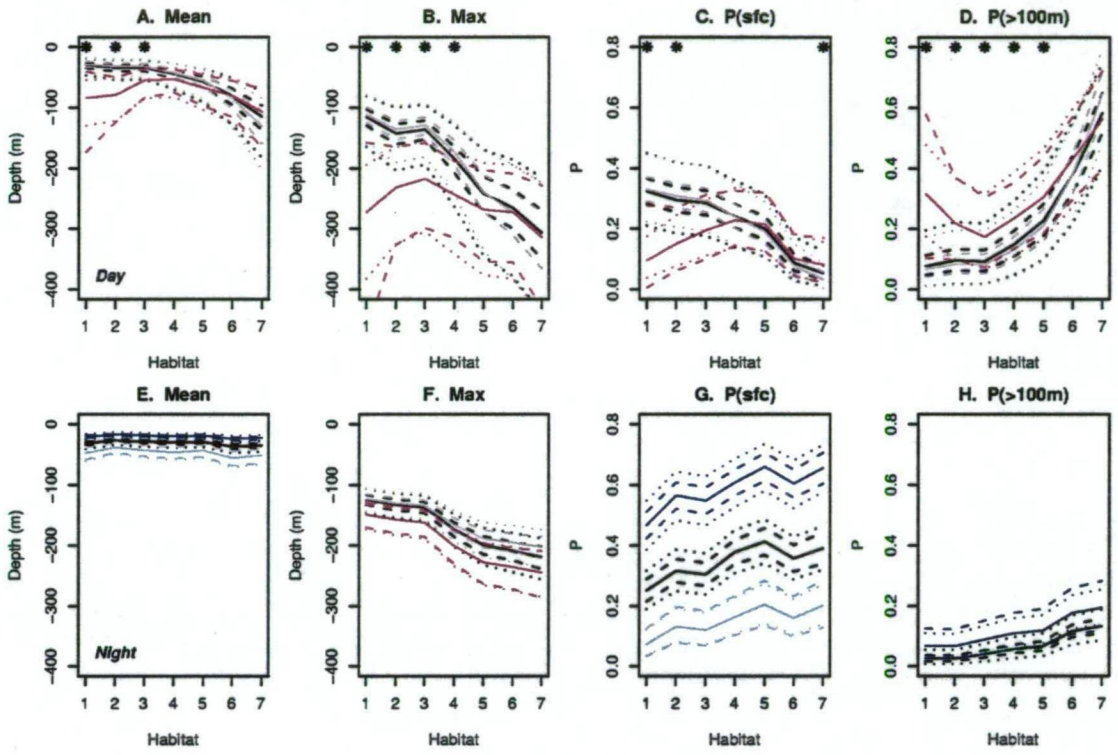

Fig. 3.6. Results of mixed-effect models including habitat, lunar phase and/or migration status as fixed effects. Final terms for each behavioural model are given in Table 3.5. For the day-time models in the upper panels (a-d) colours indicate predictions for migrating fish (magenta) and non-migrating fish (grey); (*) indicates a significant migration effect within habitat ($P < 0.01$). For the night-time models in the lower panels (e-h) colours indicate predictions for full moon (light blue), dark moon (blue), migrating (magenta), and migrating plus full moon (purple). Results are overlaid on the predictions (black) from the model including habitat only as a fixed effect (see Fig. 4).

Table 3.5. Final models following stepwise tests of lunar and migration effects on fish behaviour.

			Behavioural parameter			
	Fixed effects[a]	df	Mean	Max.	P(Sfc)	P(>100m)
Day	Habitat	7,4389	F = 501 P<0.0001	F = 1512 P<0.0001	F = 153 P<0.0001	F = 89 P<0.0001
	Habitat:Migration	7, 4389	F = 8.12 P<0.0001	F = 8.58 P<0.0001	F = 4.65 P<0.0001	F = 5.68 P<0.0001
Night[b]	Habitat	7, 4433	F = 632 P<0.0001	F = 5429 P<0.0001	F = 325 P<0.0001	F = 39.5 P<0.0001
	Migration	1, 4433	ns	F = 29.7 P<0.0001	ns	F = 21.8 P<0.0001
	Lunar	1, 4433	F = 284 P<0.0001	ns	F = 448 P<0.0001	F = 20.9 P<0.0001

[a] F-values and *P*-values are from Wald tests for the significance of model terms; ns indicates non-significance ($P > 0.01$). Anova is based on the marginal sum of squares *i.e.* obtained by deleting one term from the model at a time.
[b] Denominator degrees of freedom in the night-time P(sfc) and P(>100m) models are actually 4403 and 4402, respectively.

Figure 7 shows an example of the observed data for a single fish (SBT99-267) together with predictions from the three models (1) habitat-only, (2) habitat plus habitat as a random effect, and (3) habitat plus migration and/or lunar effect. There is a high degree of within-fish variability observable in most of the behaviour parameters, but particularly in the surfacing probabilities (Fig. 3.7c, g). As an example, from the habitat-only models the estimate of the residual variance within fish (W) was generally an order of magnitude higher than the variance of the random effects between fish (B) (*e.g.* for the day models, mean: W = 0.83, B = 0.06; max: W = 0.44, B = 0.03; P(sfc): W = 0.09, B = 0.004; P(>100m): W = 0.13, B = 0.008). Therefore, the extremes in behavioural range are in general poorly represented (*e.g.* maximum depth is often underestimated), but overall, given the relatively few predictive terms, the models do a reasonable job of capturing the salient features in the fish's behaviour.

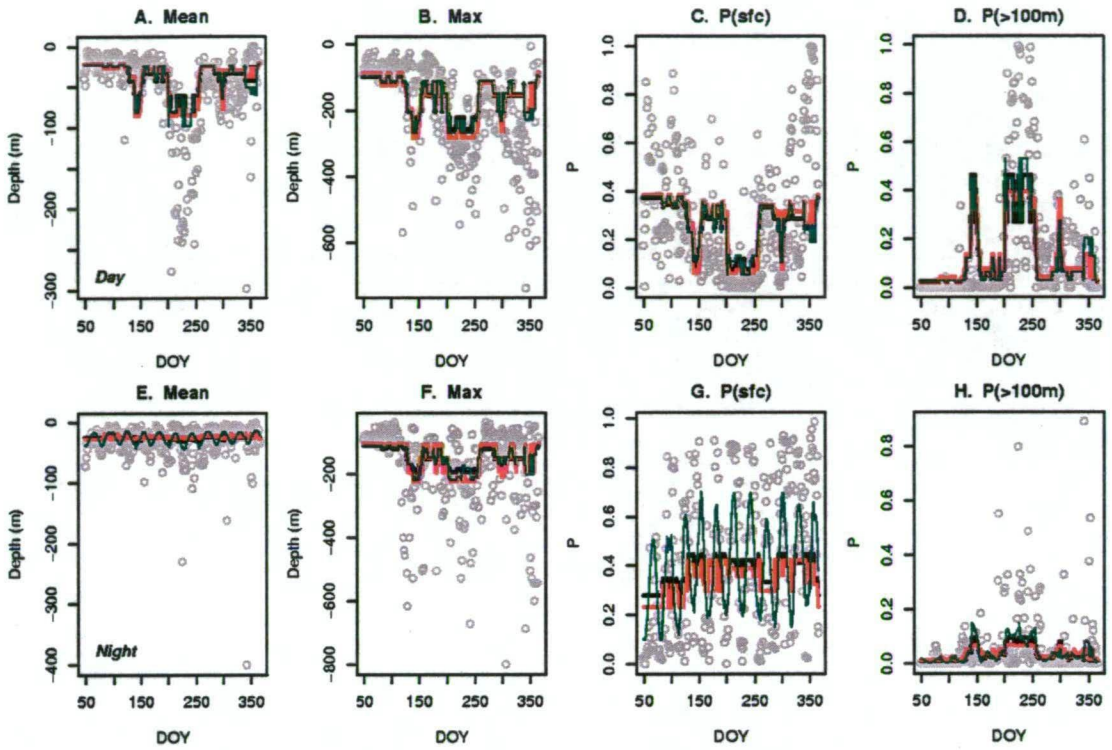

Fig. 3.7. Model predictions (lines) and observed data (circles) for an individual fish (SBT97-731) throughout an annual cycle. Day-time and night-time are shown in the upper (a-d) and lower (e-h) panels, respectively. Predictions are shown for three models: habitat as a fixed effect only (black, see Fig. 3.4), habitat as both a fixed and random effect (red, see Fig. 3.5), and habitat plus lunar and/or migration as fixed effects (green, see Fig. 3.6). DOY = day of year.

Depth and temperature niches

Figures 3.8 and 3.9 respectively show how the time spent at depth and at temperature varied between habitat types, and the general consistency of behaviour across individuals. There is no indication that SBT attempt to maintain a preferred temperature niche between habitats by adjusting their vertical movement. For example, in the warmest habitat (HAB1) juvenile SBT on average spent over 75% of their time within the restricted temperature range 19–22°C (day = 78%, night = 84%), although colder temperatures were available at depth (also the case in other habitats with a thermocline). In comparison, in the very cold HAB7 over 75% of their time was spent within the restricted temperature range 9–13°C (day = 86%, night = 76%). While little alternative was available at depth

in this habitat, alternatives were presumably available via horizontal movement choices. For non-migrating fish, a cooler temperature distribution (Fig. 3.9a-d) generally reflects a deeper distribution (Fig. 3.8a-d) in the warmer habitats, consistent with the estimates from the mixed effect models.

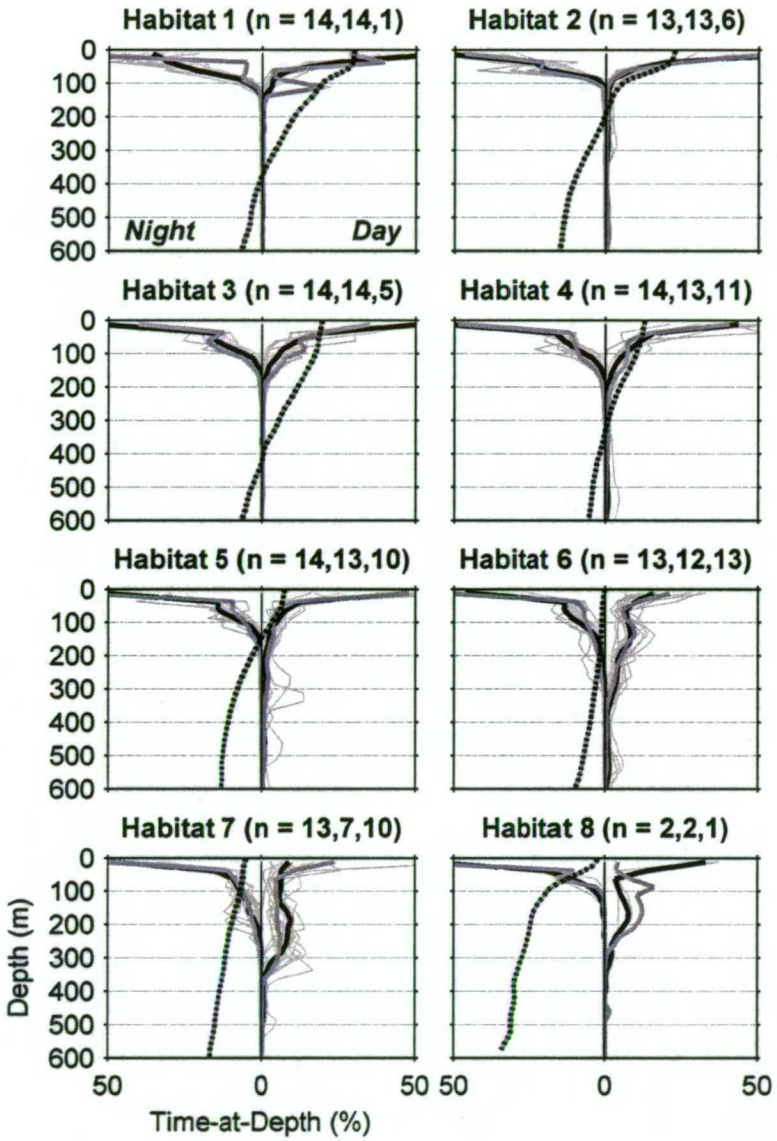

Fig. 3.8. Back-to-back histograms showing the average percentage of time spent at depth by SBT within eight oceanic habitats by night (LHS) and day (RHS). Data aggregated by 25 m depth bins with depths greater than 600 m excluded. Colours indicate non-migrating days (black bold), migrating days (grey bold) and all days from individual fish (grey). N indicates number of individuals represented in each panel: total, those with at least 3 non-migrating days, those with at least 3 migrating days. For reference the mean temperature profile for each habitat (rescaled from Fig. 3.2) is shown (dot-dash).

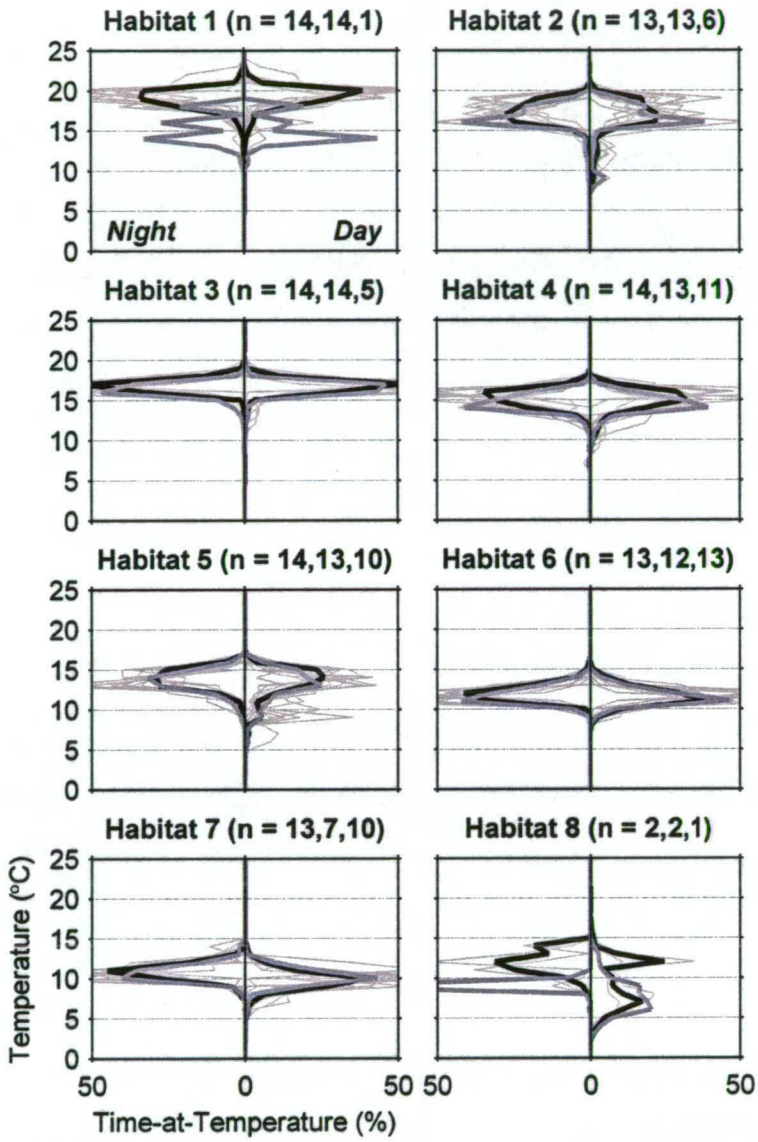

Fig. 3.9. Back-to-back histograms showing the average percentage of time spent at temperature by SBT within eight oceanic habitats by night (LHS) and day (RHS). Data aggregated by 1°C temperature bins; otherwise data representation as in Fig. 3.8.

DISCUSSION

This study used a novel method to characterise the oceanic habitats targeted by a highly migratory species during an annual migration on the basis of physical properties (using daily temperature-depth profiles). Using this approach, juvenile SBT were found to occupy eight major habitats between the southern margin of the subtropical gyre and the northern edge of the Antarctic Circumpolar Current (*i.e.* north of the Subantarctic Front) in the south Indian Ocean. While a high degree of variability in behaviour in terms of vertical position in the water column was evident both within fish and between fish, mixed effect models identified consistent behavioural responses to habitat, lunar phase, migration status and diel period, indicating there is a predictable component to vertical movement. Our results indicate SBT do not act to maintain preferred depth or temperature ranges, but in fact show highly plastic behaviours in response to their changing ocean environment.

Oceanic habitats were characterized using an exploratory method based solely on the temperature/depth data collected by archival tags (Field *et al.* 2001; Hinke *et al.* 2005b). The objective clustering approach avoided arbitrary spatial and temporal boundaries and was therefore independent of errors associated with position estimates (Hill & Braun 2001). However, the position information available indicated the habitat groups were spatially and temporally coherent at a basin-wide scale, and related well to existing descriptions of the dynamic upper thermal structure of the ocean (McCartney 1982; Nagata *et al.* 1988; Belkin & Gordon 1996; James *et al.* 2002; Kostianoy *et al.* 2004; Yuan *et al.* 2004). It should be noted that analyses at finer spatial scales, for example investigating relationships with specific mesoscale features such as eddies or local frontal features, remain limited by the resolution of geolocation methods currently available for archival tags.

Although SBT used all available habitats between 30–45°S during the course of an annual migration, migration routes were variable among individuals and typically interspersed several weeks or more in cooler waters (HAB6–7) with

a similar period in warmer waters (HAB3–4). Therefore, after moving out of the GAB summer grounds, SBT distributed throughout subtropical, subtropical mode and subantarctic waters (8–22°C SST) during the remainder of the year. Notably, throughout this range SBT did not appear to maintain preferred temperature or depth niches. Rather individuals were capable of occupying narrow (*e.g.* a thermal range of only 2–3°C), but diverse ambient temperature niches for extended periods (*e.g.* an individual may inhabit waters of 11-13°C for several weeks, then waters of 19-21°C for several weeks). However, the low visitation to the coldest Subantarctic Front habitat (HAB8), together with the lengthy residency there of one individual later as a 4-year old, suggest these temperatures may represent a thermal limit (Carey & Lawson 1973) for 3-year old SBT.

North of the Subantarctic Front, variation in the amount of time spent in each habitat appeared attributable to individual differences rather than any consistent differences in habitat availability (or preference) between years. Contemporary hydrographic survey (James *et al.* 2002; Yuan *et al.* 2004) and satellite data (Kostianoy *et al.* 2004) both indicated relatively little movement of the major oceanographic features during the study period 1998–2000. However, substantial inter-annual variation, for example in the latitudinal position of the Subtropical Front in the eastern basin particularly (Nagata *et al.* 1988), has been documented and may influence SBT migrations over longer time scales.

Habitat type was a significant factor influencing SBT behaviour, even taking the significant fish-to-fish variability into account. The linear mixed effect models showed that SBT exploited deeper day-time depths in the mode water and subantarctic habitats (*i.e.* HAB6 and HAB7) than in the subtropical habitats (particularly HAB1–4). It is unlikely the observed changes in the vertical movements of SBT are due to physical or physiological barriers. A physical bathymetric constraint seems unlikely as even the wide continental shelf of the GAB deepens to 200 m quite rapidly. It also appears unlikely that the thermocline acts as a barrier to vertical movement (Kitagawa *et al.* 2000). Firstly, the thermocline structure along the subtropical margin (HAB3–4) tends to be relatively weak in the winter months and deepened to ~100 m or below (Fig. 3.2).

In addition, 3-year old SBT were commonly found to target regions of high thermal gradient, including the strong thermoclines in HAB1–2 (Fig. 3.8) and also the temperature inversions occurring in HAB7 (data not shown). These thermal structures in the water column may in fact be important for foraging if they act to concentrate prey species (Mann & Lazier 2005). Independent of fish size, ABT have been observed to routinely expose themselves to vertical temperature changes of 14–16°C (Brill & Lutcavage 2001; Wilson *et al.* 2005), which is larger than the maximum vertical changes (~12°C) occurring within the various south Indian Ocean habitats of juvenile SBT in this study.

We hypothesise the differences in behaviour between the subtropical and subantarctic habitats are rather due to ecological factors, and relate largely to differences in the SBT prey field. Along the subtropical margin the near-surface primary production, as determined from satellite (Machu & Garcon 2001) and model (Machu *et al.* 2005) estimates, is observed to be at a maximum during the winter. The usually oligotrophic conditions are relieved due to nutrient re-supply, allowing enhanced phytoplankton growth (Machu *et al.* 2005). These conditions potentially provide the basis for rapid development of trophic webs and hence trophic transfer to higher order predators. In contrast, the pattern of productivity is reversed further south where deep wind-driven overturning and low light availability inhibits primary production in the winter and leads to a strong burst of growth during the following spring (Machu & Garcon 2001; Machu *et al.* 2005). The vertical behaviour of SBT within the subtropical habitats (HAB3–4) locates them predominantly within the epipelagic ecosystem, whereas within the mode water and subantarctic habitats (HAB6–7) they target both the epipelagic and mesopelagic regions of the water column, suggesting a different ecosystem dynamic. SBT are highly opportunistic feeders, and in the Tasman Sea eat a relatively higher proportion of squid in cooler subantarctic waters (≤14°C) than in the warmer (≥16°C) East Australia Current (Young *et al.* 1997). The changes in vertical behaviour documented here between the subtropical and subantarctic habitats of the south Indian Ocean may relate to a similar dietary shift, and reflect diurnal vertical migrations of mesopelagic prey species (Josse, Bach & Dagorn

1998). Further study on the regional trophic ecology of SBT is necessary to determine the relative importance of epi- and meso-pelagic prey items between habitats.

The vertical movements of SBT also differed significantly between migrating and non-migrating (or resident) fish. During migration, SBT tended to have deeper vertical movements, particularly during the day-time within warmer habitats. These fish also increased the maximum depth and the proportion of time at depths below 100 m recorded during the night across habitats. Notably, of the 14 tagged individuals only the outbound migration legs (*i.e.* westward from the GAB) were available from seven (50%) due to tag failure (n = 5) or high-seas recapture (n = 2), and an incomplete return migration leg was recorded by another two, again due to electronic tag failure. Therefore, the majority of recorded migration days represented westward movements against the prevailing strong eastward surface currents (Belkin & Gordon 1996). A number of recent studies tracking migratory pelagic predators have proposed associations with oceanic currents, or 'hitchhiking', as a mechanism for reducing transport costs (Clarke *et al.* 2003; Ream, Sterling & Loughlin 2005). The pattern observed here may represent the opposite, *i.e.* a reduction in transport costs obtained via the submergence of SBT below the strong surface currents during westward migrations, and/or relate to other energy-saving swimming patterns (Weihs 1973). However, the mechanisms by which SBT navigate their migratory routes remain unknown. The changes in vertical behaviour may also reflect movement to detect different strata of the water column (Arnold 1974) or magnetic fields (Walker 1984) and thus help in guiding migratory movements.

Lunar phase was a highly significant factor influencing night-time vertical behaviour, with a full moon consistently deepening SBT distributions across all habitat types, a result further strengthening our ecological interpretation of SBT vertical behaviour. Similar strong lunar influences have been widely reported among tunas (Schaefer & Fuller 2002; Wilson *et al.* 2005), with deeper diving patterns around a full moon generally thought to mirror the movements of nocturnally migrating prey organisms in the deep scattering layer (DSL), which in

turn are following isolumes (Josse *et al.* 1998; Schaefer & Fuller 2002). The available evidence, although largely anecdotal, indicates that SBT are primarily visual predators and have a feeding peak around sunrise (Young *et al.* 1997). The synchronous response of SBT to the moon may therefore indicate that enhanced night-time foraging opportunities are afforded by the increased lunar illumination, or perhaps that SBT follow the DSL to obtain an advantageous ambush position for the coming dawn. Both scenarios are consistent with Australian longline catch per unit effort data showing intensified fishing effort around the full moon, and observer reports ranking moon phase as the second most important fishing indicator after temperature (Lyne *et al.* 1999).

As a consequence of the strong lunar effect, SBT cannot be generally characterized as having consistent day-night differences in vertical distribution. The only pronounced diurnal patterns occurred in the subantarctic waters (HAB7) and to a lesser degree in the mode water region (HAB6), where fish tended to be deeper during the day. This deep diurnal pattern is similar to that reported for species known to closely track the DSL. Interestingly however, in the GAB (HAB1) the mixed effect models also indicated deeper average depths and reduced surfacing during the night-time compared with the day-time (Fig. 3.4). Although statistically non-significant, these patterns were further amplified on the full moon and hint at another level of behavioural complexity in juvenile SBT *i.e.* a reversed behaviour. On warm, still days in the GAB, SBT aggregate in large schools at the surface, ('rippling', Gunn & Block 2001), an event similar to the 'show days' reported for ABT schooling in the Gulf of Maine (Lutcavage & Kraus 1995). It is this strong day-time surface schooling behaviour that supports the Australian purse seine fleet, and although distinctly different from the vertical behaviours shown in the other oceanic habitats, the relatively small vertical scale of the change means it is not completely captured by the models used here.

The movement and behaviour patterns revealed by the archival tags present a number of significant challenges for the conventional use of fisheries data to estimate abundance trends (Hilborn & Walters 1992). For SBT, time series of Japanese longline catch rates form the primary index of abundance used in the

stock assessments. The migration of individuals has obvious implications for the relative availability of SBT, *i.e.* the proportion of the population present within a fishery region. Catch rates will reflect movement of animals through an area as well as local density. Additionally, SBT are clearly vulnerable to multiple fleets. Within the south Indian Ocean these are namely: the Australian purse-seine fleet in the GAB; the Japanese longline fleet predominantly in the eastern and western basins; and the Taiwanese longline fleet which operates primarily along the subtropical margin. The high degree of behavioural flexibility displayed by SBT throughout their range of habitats has further implications for their catchability, *i.e.* their vulnerability to fishing gears, and how the effectiveness of a unit of fishing effort will vary in space and time.

Recently, attempts have been made to develop models for tunas and billfish which standardize catch-per-unit-effort data accounting for how fish behaviour affects catchability. Most usually these models incorporate information on "habitat" preferences such as preferred temperature and/or depth ranges obtained from electronic tag sources (Bigelow *et al.* 2002; Kleiber *et al.* 2003). This approach has come under some criticism because of the simplistic assumptions about fish behaviour, and the sensitivity of the models to those assumptions (Goodyear 2003). Indeed, our results indicate such an application would not be straightforward for a species such as SBT, whose complex behavioural patterns would not be easily represented using either temporal or spatial strata (*e.g.* season/area). For example, within a season SBT vertical distributions vary significantly between habitats, and the spatial boundaries between habitats in a dynamic ocean can vary both seasonally and inter-annually. However, the use of direct observation to identify correlations between fish behaviour and environmental conditions is a significant first step in the development of predictive models for the movement and depth distribution of highly mobile pelagic species (Bigelow & Maunder 2007). Our study demonstrates the potential power of these tags to provide the habitat-specific data necessary to integrate the spatial and temporal interaction between the SBT population and fishery into the interpretation of catch rate trends.

Our results suggest there may be a hierarchy in the factors influencing SBT vertical distributions. Lunar phase appeared to be an important influence on SBT behaviour throughout their range, whereas the physical structure of the oceanic habitat determined regionally different behaviours, and the influence of diel period and migration period varied depending on habitat. The high level of within-fish variation is likely to reflect even more localized processes not resolved in this analysis, such as the location and density of the local prey field and other sub-habitat processes. Surfacing behaviour in particular is likely to be sensitive to local climate (*e.g.* wind, swell, turbidity, cloud cover). More broadly, it may be that edge effects are important, *i.e.* that SBT behavioural changes near the frontal boundaries between habitats are significant (Olson *et al.* 1994). The effect of meso-scale variability in the Agulhas region on ecosystem structure (Read *et al.* 2000) and predator behaviour (Nel *et al.* 2001) may also be significant, yet data from this area is currently subsumed within the larger habitat groupings. Nevertheless, the habitats characterised in this study proved useful for evaluating the timing and nature of SBT behavioural changes over a spatial scale of thousands of kilometres and yet interpreting these changes directly in relation to the fish's immediate environment.

CONCLUSIONS

In summary, this study has provided significant new information on changing patterns of habitat utilization by juvenile southern bluefin tuna throughout their migratory range. Behavioural responses to oceanic and environmental factors have been directly quantified, and possible mechanisms underlying the observed relationships proposed. Our results are consistent with the description of a highly opportunistic predator, capable of exploiting a variety of ecological niches throughout subtropical to subantarctic waters. However, further research on feeding behaviour is required to clarify the behaviours elucidated in this study and the trophic role of SBT within the various ecosystems of the South Indian Ocean, and hence provide insight into the motivations behind these extraordinary long-distance migrations.

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4. Feeding ecology of wild migratory tunas revealed by archival tag records of visceral warming

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ABSTRACT

Seasonal long-distance migrations are often expected to be related to resource distribution and foraging theory predicts that animals should spend more time in areas with relatively richer resources. Yet for highly migratory marine species data on feeding success are difficult to obtain. We analysed the temporal feeding patterns of wild juvenile southern bluefin tuna from visceral warming patterns recorded by archival tags implanted within the body cavity. Data collected during 1998–2000 totalled 6221 days, with individual time-series (n = 19) varying from 141 to 496 days. These data span an annual migration circuit including a coastal summer residency within Australian waters and subsequent migration into the temperate south Indian Ocean. Individual fish recommenced feeding between 5 and 38 days after tagging, and feeding events (n = 5194) were subsequently identified on 76.3 ± 5.8% of days giving a mean estimated daily intake of 0.75 ± 0.05 kg. The number of feeding events varied significantly with time of day with the greatest number occurring around dawn (58.2 ± 8.0%). Night feeding, although rare (5.7 ± 1.3%), was linked to the full moon quarter. Southern bluefin tuna foraged in ambient water temperatures ranging from 4.9°C to 22.9°C and depths ranging from the surface to 672 m, with different targeting strategies evident between seasons. No clear relationship was found between feeding success and time spent within an area. This was primarily due to high individual variability, with both positive and negative relationships observed at all spatial scales examined (grid ranges of 2 x 2° to 10 x 10°). Under the assumption that feeding success is proportional to forage density, our data do not support the hypothesis that these predators concentrate their activity only in areas of higher resource availability. Multiple-day fasting periods were recorded by most individuals. The majority of these (87.8%) occurred during periods of apparent residency within warmer waters (sea surface temperature > 15°C) at the northern edge of the observed migratory range. These previously undocumented non-feeding periods may indicate alternate motivations for residency. Our results demonstrate the importance of obtaining information on feeding when interpreting habitat utilisation from individual animal tracks.

Chapter 4

INTRODUCTION

Understanding the movement of animals in time and space and its implications for the abundance and distribution of populations is a pivotal problem in animal ecology, fundamental to conservation and resource management strategies. Migration is often a response to environmental heterogeneity, such as adaptations to seasonal cycles in weather patterns and resource availability (Alerstam *et al.* 2003). For immature or non-breeding individuals, the resources driving movement generally relate to food supply and/or habitat suitability (Baker 1978). Modern telemetry has provided data on individual movements of highly mobile marine animals previously difficult to study due to their speed and the vast range over which they travel (Ropert-Coudert & Wilson 2005; Hays 2008). Direct links between movement patterns and food resources have been difficult to establish, due to a lack of explicit information on food availability, foraging activity and feeding success.

In the oceanic environment resources are patchily distributed at a range of spatial and temporal scales and predators must successfully locate prey in a three-dimensional habitat (Hindell *et al.* 2002). Foraging theory predicts that animals should spend more time in areas of high foraging success, and should minimise time spent moving between these areas (Stephens & Krebs 1986). Although the interpretation of individual movement data has proved to be a non-trivial task (Turchin 1998), time spent in an area is commonly used as a convenient way to represent data from multiple individuals or species (Guinet *et al.* 2001; Bradshaw *et al.* 2004b). Habitat utilisation by marine predators is widely assumed to reflect the quality and availability of resources in an area, with areas of high use popularly inferred to be areas of high foraging success (Bailey & Thompson 2006). From this premise ensues an increasing effort to identify oceanic regions of enhanced biological productivity of interest to predators (Sydeman *et al.* 2006), often with objectives relating to conservation zoning and fisheries management. However the assumption that areas of highest residency correspond to feeding areas has remained largely untested in the absence of direct feeding data.

Direct observation of feeding is generally not possible for large marine predators as they forage over large and remote areas and commonly whilst diving. Hence information on when and how feeding actually occurs is commonly inferred indirectly from behavioural information such as vertical diving (Boyd & Croxall 1996), landing events in seabirds (Shaffer, Costa & Weimerskirch 2001) or movement patterns (Jonsen, Flenming & Myers 2005; Robinson *et al.* 2007). There are a number of methods for directly establishing feeding rates for marine vertebrates. Motion sensors attached to the jaws can reveal feeding patterns over periods of a few days (Fossette *et al.* 2008). For cetaceans that use echolocation to locate prey, loggers recording ambient sounds may reveal prey pursuit and capture (Watwood *et al.* 2006). However, for longer-term records of feeding perhaps the most widely used technique is to measure stomach or oesophageal temperature (Gales & Renouf 1993; Austin *et al.* 2006a). Yet stomach telemetry is often hampered by the premature ejection of sensors from the stomach.

In bluefin tunas the visceral temperatures increase markedly in association with digestion (Carey *et al.* 1984). This is thought to be due to a combination of factors, but probably most important is the heat produced by specific dynamic action (*i.e.* the result of metabolic heat production during digestion). The elevated temperatures promote increased enzyme activity (Stevens & McLeese 1984) and appear to be the primary mechanism by which tunas digest food much faster than other piscivorous fish. In cage experiments, archival tags incorporating a temperature sensor implanted within the body cavity of southern bluefin tuna (*Thunnus maccoyii*) and Pacific bluefin tuna (*T. orientalis*) showed regular patterns of visceral warming and cooling, providing an accurate record of when feeding events occurred (Gunn *et al.* 2001; Itoh *et al.* 2003b). These patterns also occur in data collected from wild fish (Gunn & Block 2001; Itoh *et al.* 2003b; Kitagawa *et al.* 2004).

For adult animals, long distance migrations are often associated with travel to breeding sites. This means that tracking often simply reveals shuttling between breeding and foraging sites, rather than specifically animal search for prey patches (Hays *et al.* 2006; Bailey *et al.* 2008). Tracks of juveniles, being non-breeding, might therefore be expected to be more tightly coupled to food resources. We

used long-term archival tag records of visceral warming to examine the temporal feeding patterns and seasonal foraging ecology of wild juvenile southern bluefin tuna (SBT) during their migrations in the south Indian Ocean. Specifically, we examined the hypothesis that highly mobile species should spend more time in energetically profitable areas, by examining the relationship between the feeding success of SBT and the time spent in specific areas. The rare combination of long-term feeding and movement data allows for a unique interpretation of habitat utilisation by a highly migratory marine predator.

METHODS

Data collection and processing

Archival tag data

During the austral summers of 1998–2000 SBT (n = 200) were caught by pole-and-line in the Great Australia Bight (GAB) and archival tags of model Mk7 (Wildlife Computers, Redmond, WA) were surgically implanted into the peritoneal cavity ventral to the stomach. Tags sampled pressure (depth), ambient light, ambient water and visceral temperatures every 4 minutes. To date, 51 (25.5%) have been recovered and data retrieved from 47. Due to very early recapture (n = 10), or sensor (n = 4) and tag (n = 4) failures, long-term (> 120 days) data were obtained from only 29.

Location estimation

Daily longitudes were determined by geolocation methods (Hill 1994) using GeoControl software v2.01.0002 (Wildlife Computers). Nineteen age-3 fish (mean fork length = 99 ± 3 cm, range = 93–111 cm) (Eveson *et al.* 2004) moved west into the south Indian Ocean during their first year at liberty, and these migrants are the focus of this analysis. Latitude was estimated by comparing the surface water temperature recorded by the tag with satellite SST estimates (Teo *et al.* 2004). Briefly, using the Advanced Very High Resolution Radiometer (AVHRR) weekly global 18 km multichannel SST (MCSST) (night passes) data (http://podaac.jpl.nasa.gov/PRODUCTS/p016.html), a strip centred on the geolocation longitude (± 1°E) was searched from 20°S–60°S. Shown in this analysis are the median positions of all MCSST pixels matching within ± 0.2°C of the median temperature recorded in the surface 5 m during each 24 h. Using this method the average 90th percentile boundaries of all pixel matches are 1.1 and 0.8 degrees to the north and south of the median position respectively.

Determining the time of feeding events and relative meal size

The visceral warming recorded by the internal temperature sensor on tags (Fig. 4.1) provided a record of (a) feeding incidence, and (b) a means of estimating relative intake mass. The data were viewed over 48 h windows and a basal temperature calculated. The start of a feeding event was identified by either (a) a sharp dip in visceral temperature (associated with the ingestion of cold food and/or water) followed by a steep steady rise above the initial temperature, or (b) a steep steady rise not preceded by a dip. The simultaneous ambient temperature and depth records were used to evaluate whether observed changes were from moving into cooler water. A feeding event was considered to have ended when the visceral temperature passed the maximum rise and (a) returned to basal, (b) dropped to a new plateau, or (c) changed in a manner indicative of the start of another feed.

In SBT there is a robust relationship between total intake size (of prey in grams) and the time taken to reach the maximum heat increment above basal (T_{max}, Fig. 4.1) (Gunn *et al.* 2001). However this relationship was developed from a single prey type (pilchards), and the type and relative importance of baitfish in SBT diet is known to be regionally variable *e.g.* from >80% to <50% weight (Young *et al.* 1997). Furthermore, the effects of varying prey type (*e.g.* fish c.f. squid) and energy density or composition (*e.g.* lipid content) on the slope of this relationship are unknown and likely to be substantial (Olson & Boggs 1986). For example, there may be the possibility of non-detectable feeding events from very small and quickly digestible prey items, or (high water content) prey types that produce almost no temperature signature. In addition, the maximum attainable visceral temperature is not yet known for any bluefin species. There remains a critical need for different experiments to test such uncertainties on the method, and these form the substantive part of other PhD theses currently underway (D. Ellis, *pers. comm.*, University of Tasmania) or as yet unpublished (A. Walli, Stanford University). Therefore, it is important to stress the use of this data as a *relative* quantitative index of intake size only, and all quantitative predictive models are restricted to using counts or presence/absence of feeding events. Results are reported as mean ± S.D. across individual fish unless otherwise stated.

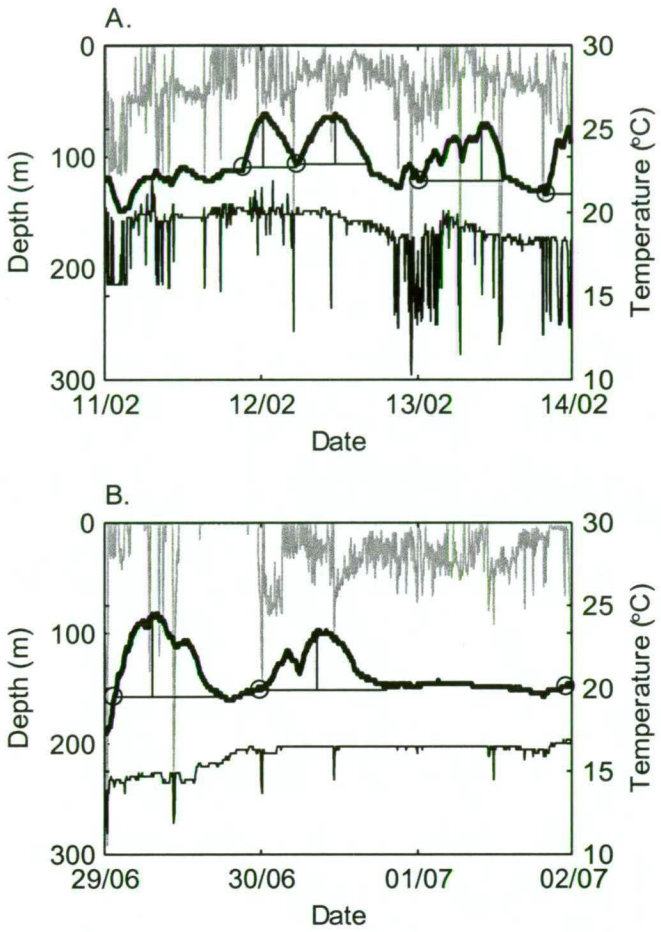

Fig. 4.1. Example of archival tag time-series showing visceral warming patterns recorded by the internal temperature sensor (bold black line). Circles indicate commencement of a feed, horizontal lines indicate feed duration and vertical lines indicate time at which the maximum heat increment is reached (T_{max}). Vertical swimming depth (grey) and ambient water temperature (black) are also shown. (a) First feeding events of SBT97639 17 days post-tagging in the Great Australia Bight during the austral summer; (b) SBT97622 in the central south Indian Ocean (97–98°E, 34–35°S) during the austral winter.

Data analysis

Temporal feeding patterns

To investigate temporal patterns in feeding, we examined both moon-quarter and time of day. Lunar illumination for a given date was calculated using standard astronomical equations and feeding events aggregated into the four periods of dark, waxing, full and waning. Time of day was also aggregated into four periods. Feeding events initiated within 2 h either side of dawn or dusk were defined as such. While these periods each spanned 4 h per 24 h, the day and night lengths varied seasonally.

To test for the effects of moon quarter and time of day on feeding frequency, generalised linear mixed models (GLMMs) were used where the random effect was the individual fish and the error distribution was Poisson with a log link function. To determine the best predictive model, the GLMM having the lowest Akaike's Information Criterion (AIC) was selected. The models were fit by maximising the log-likelihood using the Laplacian approximation. Therefore, to evaluate the properties of individual coefficients we sampled from the posterior distribution of the parameters of the best predictive model using Markov Chain Monte Carlo methods (n = 20000, using function mcmcsamp in R package lme4). The prior on the fixed effects parameters is taken to be locally uniform. Reported are the mean estimate ± S.D. together with the 95% highest posterior density (HPD) intervals and associated empirical P-value. All statistical analyses were carried out using R-software v2.5.1 (R Development Core Team, 2007), with the GLMMs fitted in the package lme4 v0.99875-6 (Bates 2007).

Foraging ecology

To investigate whether the foraging ecology of juvenile SBT changed seasonally we examined the water temperature and depth data, recorded by the tag, associated with the start of each feeding event. Linear mixed models were used where season was fitted as both a fixed and a random effect. The models were fit using restricted maximum likelihood estimation (REML). Reported F-values and

P-values are based on Wald tests. In case of a lag between prey capture and the start of visceral warming the models were refit to the data from the previous timestamp (*i.e.* the temperature and depth records 4 minutes prior to the estimated start time) but there were no substantive differences. The LMMs were fitted in the R package nlme v3.1-83 (Pinheiro *et al.* 2007).

Feeding and residency

To examine the relationship between feeding success and time spent in an area we gridded the daily position estimates at various spatial scales. To take into account the error associated with the geolocation methods the smallest grid used was 2 x 2° in size, ranging up to a 10 x 10° grid. The number of successful/unsuccessful feeding days was then modelled in response to the total number of days spent per square, using a generalised linear model with a binomial error distribution and a logit link function. This model was fit to the original data aggregated across fishes and a bootstrap validation run to ascertain validity across fishes, in which all fish (and all their data points) were sampled with replacement and the model refit (n = 10000). To investigate further the pattern for individual fish, we examined GLMMs with a binomial error distribution. Data from squares centred within the GAB coastal summer residency area bounded by the coordinates [127.5°E, 29°S], [127.5°E, 34°S], [140°E, 34°S], [140°E, 42.5°S] (Fig. 4.4) were excluded from this analysis. Fish with data available only for the outward migration leg from the GAB *i.e.* without any oceanic residencies, due to early tag failure (n = 3) or recapture (n = 1), were also excluded.

RESULTS

A total of 6221 days of data were collected from the 19 fish, with individual time-series spanning 141–496 days (Table 4.1). Individuals recommenced feeding between 5 and 38 days after tagging (mean ± SD: 19 ± 10 days). These post-release fasting periods were excluded from all analyses. Feeding events (n = 5194) were subsequently identified on 76.3 ± 5.8% of days (range: 63.5–84.9%), for an overall feeding rate of 0.89 ± 0.08 feeding events per day per individual (range: 0.76–1.16). On feeding days, the feeding rate was 1.17 ± 0.09 (range: 1.05–1.48). The estimated daily intake was 0.75 ± 0.05 kg (range: 0.67–0.85 kg) and the mean feed size was 0.85 ± 0.09 kg (range: 0.63–1.03). The mean duration of the visceral temperature signature associated with a feeding event was 18.5 ± 1.4 h (range: 14.4 - 20.9). The minimum interval recorded between feeding events was 40 min, however there was a distinct diurnal cycle with the median ranging between 18.7–24.1 h. There was considerable variation in the maximum between-feed interval, with individuals recording periods of up to 3.9–24.4 days without feeding (mean ± SD: 11.4 ± 6.5).

Temporal patterns in feeding

The number of feeding events varied strongly with time of the day (GLMM, all $|z| > 24$, $P < 0.0001$; Table 4.2) with the highest number of feeding events (58.2 ± 8.0%) and feeding rate (0.16 ± 0.03 feeds h^{-1}) occurring near dawn (Fig. 4.2a). Some feeding activity occurred during the day (26.0 ± 6.4%) but rarely at night (5.7 ± 1.3%, Fig. 4.2a). Moon quarter was not a significant independent factor influencing the number of feeding events (GLMM, all $|z| < 1$, $P > 0.3$), however the moon quarter-time of day interaction was significant (Table 4.2). Night feeds during the full moon quarter were predicted to be more likely by a factor of 10.7 (± 1.3, 95%HPD = 6.2–19.6, $P < 0.0001$) relative to the dark moon, and by a factor of 5.6 (± 1.4, 95%HPD = 3.1–10.2, $P < 0.0001$) and 3.3 (± 1.4 SE, 95%HPD = 1.8–6.3, $P = 0.0001$) during the waning and waxing quarters, respectively (Fig. 4.2b). A weaker effect of the full moon was a small decline in dawn feeding (by a factor of 0.8 ± 1.1, 95%HPD = 0.7–0.9, $P = 0.0001$) and

increase in day and dusk feeding (by a factor of 1.5 ± 1.1, 95%HPD = 1.2–1.8, $P < 0.0001$ and 1.6 ± 1.1, 95%HPD = 1.3–2.0, $P = 0.0001$ respectively). The best model explicitly included a random effect for time of day within fishes, due to small variations in relative feed incidence between day and dusk.

Table 4.1. Feeding information obtained for 19 wild juvenile SBT based on visceral temperature patterns.

SBT ID	Record length (days)	Post-surgery fast* (days)	Days with feeding (days)	Total feeds	Feeding rate (feeds day^{-1})	Daily intake† (kg)
97622	409	36	258 (69.2%)	324	0.87	0.75
97682	332	21	244 (78.5%)	284	0.91	0.79
97708	247	20	168 (74.0%)	206	0.91	0.78
97721	338	32	221 (72.2%)	251	0.82	0.77
97615	227	31	165 (84.2%)	191	0.97	0.67
97639	496	17	378 (78.9%)	412	0.86	0.69
97718	209	15	152 (78.4%)	225	1.16	0.73
97733	332	19	231 (73.8%)	280	0.89	0.77
97741	252	13	188 (78.7%)	216	0.9	0.84
98007	389	38	235 (67.0%)	266	0.76	0.78
97731	490	11	370 (77.2%)	442	0.92	0.85
98553	335	17	254 (79.9%)	283	0.89	0.8
98556	316	31	181 (63.5%)	222	0.78	0.71
98574	141	20	93 (76.9%)	104	0.86	0.76
99267	454	6	349 (77.9%)	408	0.91	0.7
99626	370	5	259 (71.0%)	301	0.82	0.7
99627	341	10	267 (80.7%)	294	0.89	0.76
99629	297	5	248 (84.9%)	283	0.97	0.79
99664	246	15	193 (83.5%)	202	0.87	0.71
Mean ± SD		19 ± 10	(76.3 ± 5.8%)		0.89 ± 0.08	0.75 ± 0.05
Range	141–496	5–38	(63.5–84.9%)		0.76–1.16	0.67–0.85
Total	6221	362	4454	5194		

† Daily intake calculated from the relationship with time to maximum temperature, $T_{max} = 0.5845 *$ Intake (g) (Gunn et al, 2001).

* Data from this post-surgery period was excluded from all subsequent calculations and analyses.

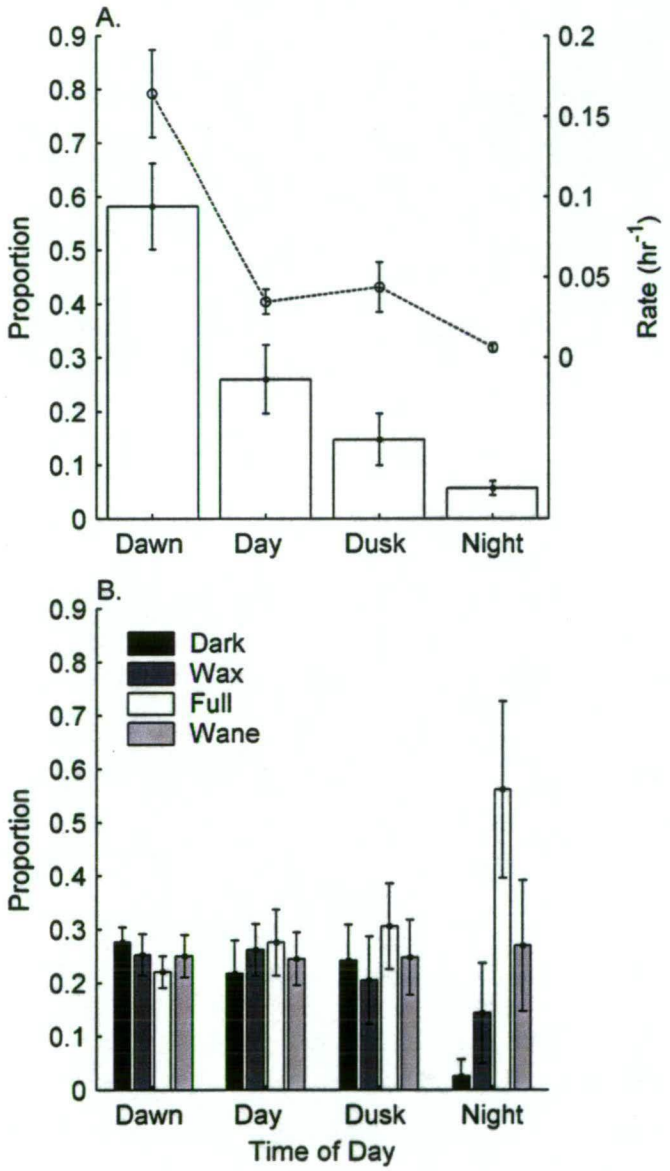

Fig. 4.2. Frequency of feeding events by (a) time of day, and (b) moon quarter. Feeding rate (feeds hr^{-1}) by time of day is also shown (dashed line) in (a).

Table 4.2. Results for generalized linear mixed models (GLMM) with time of day and moon quarter as factors affecting feeding frequency. The best fit was determined according to the lowest Akaike's information Criterion (AIC). Scale = the estimated scale parameter (ideally close to 1); df = degrees of freedom; LL = log-likelihood; ΔAIC = the difference in AIC from that of the best-fitting model.

GLMM[†]		Scale	*df*	LL	AIC	ΔAIC
Fixed effects	Random effects					
(a) Time of Day (TOD)	Intercept	1.475	5	-361.2	732.3	204.2
(b) Moon Quarter (MQ)	Intercept	3.496	5	-1928.9	3867.7	3339.6
(c) TOD + MQ	Intercept	1.469	8	-360.5	737	208.9
(d) TOD + MQ + (TOD x MQ)	Intercept	1.311	17	-297.6	629.2	101.1
(e) TOD + MQ + (TOD x MQ)	Intercept + TOD	1.038	27	-237.1	528.1	0
(f) TOD + MQ + (TOD x MQ)	Intercept + MQ	1.311	27	-297.6	649.2	121.1

[†] $n = 5179$ *i.e.* 5194 total feeds less 15 feeds with TOD unknown due to light sensor failure

Seasonal feeding ecology

Comparison of the seasonal temperature-depth habitat of SBT (Fig. 4.3b-e) and where feeding occurred (Fig. 4.3f-i) showed similarity in the core areas, but in general a wider habitat envelope. Individuals foraged in ambient water temperatures (Fig. 4.3) ranging from a minimum of 4.9–11.3°C (9.0 ± 1.4) to a maximum of 19.3–22.9°C (20.9 ± 0.8). The maximum depth records associated with the start of feeding events ranged between 247–672 m (460 ± 134 m), and all fish recorded feed events within the surface 2 m. In summer, 41.8% (± 11.8), 55.2% (± 9.2) and 3.0% (± 6.2) of SBT feeds were initiated within the surface (0–10 m), epipelagic (10–150 m) and mesopelagic (> 150 m) layers of the water column. In winter these proportions changed to 17.5% (± 7.9), 58.5% (± 10.4) and 24.0% (± 13.2) respectively.

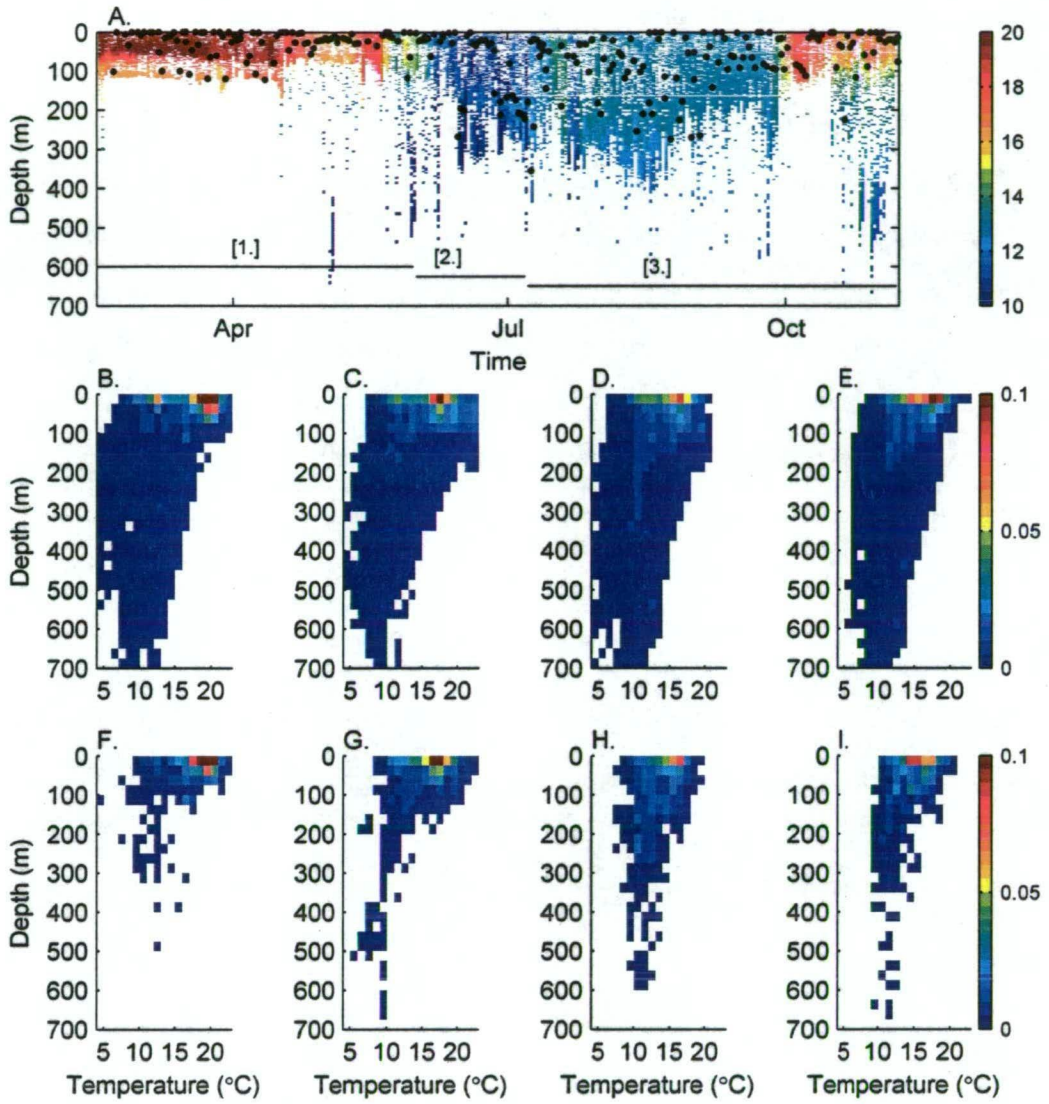

Fig. 4.3. Seasonal feeding ecology in relation to depth (m) and temperature (°C). (a) Time-series for an individual fish (SBT99629) showing locations where a feed event was initiated within the water column (black circles) during the summer GAB residency [1.], a period of rapid westward migration [2.], and winter-spring within the central (70–90°E) south Indian Ocean [3.]. Background shows ambient water temperature (°C) at depth. Remaining panels show seasonal (b-e) habitat use, and (f-i) occurrence of feeding events, by depth (25 m bins) and temperature (1°C bins) for the austral (b, f) summer (Jan–Mar, $N = 18$ fish, $n = 1058$ feeds), (c, g) autumn (Apr–Jun, $N = 19$, $n = 1716$), (d, h) winter (Jul–Sep, $N = 19$, $n = 1419$), and (e, i) spring (Oct–Dec, $N = 15$, $n = 1000$). Data in (b)–(i) are aggregated as average proportions across fishes

The seasonal differences in SBT foraging ecology were significant with respect to both the ambient water temperature ($F = 41.7$, $P < .0001$) and depth ($F = 26.0$, $P < .0001$) in which feeding events occurred (Fig. 4.3; Table 4.3). As expected, the temperature records showed a shift from feeding in warm summer (18.0 ± 0.4°C) to cooler winter (13.6 ± 0.2°C) temperatures. This coincided with a shift from shallow summer feeding (29.6 ± 4.6 m) to deeper winter foraging (96.6 ± 8.5 m) near the bottom of the epipelagic layer. The highest variance in feed temperatures between fish occurred in autumn and summer, likely reflecting both stronger vertical stratification and a higher range of near-surface temperatures in these seasons (Fig. 4.3a and b). In contrast winter showed both the lowest variance in feed temperatures and the highest variance in feed depths, reflecting the more homogeneous temperatures and expanded range of depths SBT foraged in during this season (Fig. 4.3c).

Table 4.3. Parameter estimates from linear mixed models with season as a factor affecting the temperature (°C) and depth (m) at which feed events occur.

Response	Season	σ_{fs}*	Estimate	SE	95% CI
Temperature†	Summer	1.71	17.99	0.41	17.19–18.78
	Autumn	1.84	15.51	0.43	14.68–16.34
	Winter	1.00	13.56	0.24	13.09–14.02
	Spring	1.26	14.78	0.33	14.12–15.43
Depth	Summer	15.73	29.62	4.59	20.62–38.62
	Autumn	28.53	48.63	6.86	35.18–62.09
	Winter	35.40	96.63	8.45	80.07–113.19
	Spring	27.63	69.33	7.35	54.92–83.75

† $n = 5139$ *i.e.* 5194 total feeds less 55 feeds with temperature unknown due to external temperature sensor failure

* The between-fish (f) within-season (s) random effect modelled as a random normal variable $\sim N(0, \sigma^2_{fs})$

Feeding and residency

The length of time fish spent in an area showed no clear relationship to their success in feeding. Three example tracks (Fig. 4.4) demonstrate how in some instances the aggregated positions of individual fish appeared to correspond with enhanced feeding rates, and in others to correspond with reduced feeding. The data aggregated across fishes showed some spatial structuring outside of the GAB with a high number of days per square recorded around the south-west corner of Australia, in the central south Indian Ocean near [40°S, 80°E], in some areas along the subtropical latitudes (*i.e.* along 30°S) and in the far western basin (Fig. 4.5a). However, daily feeding frequency and intake showed generally high success throughout the more southerly latitudes (Fig. 4.5b and c).

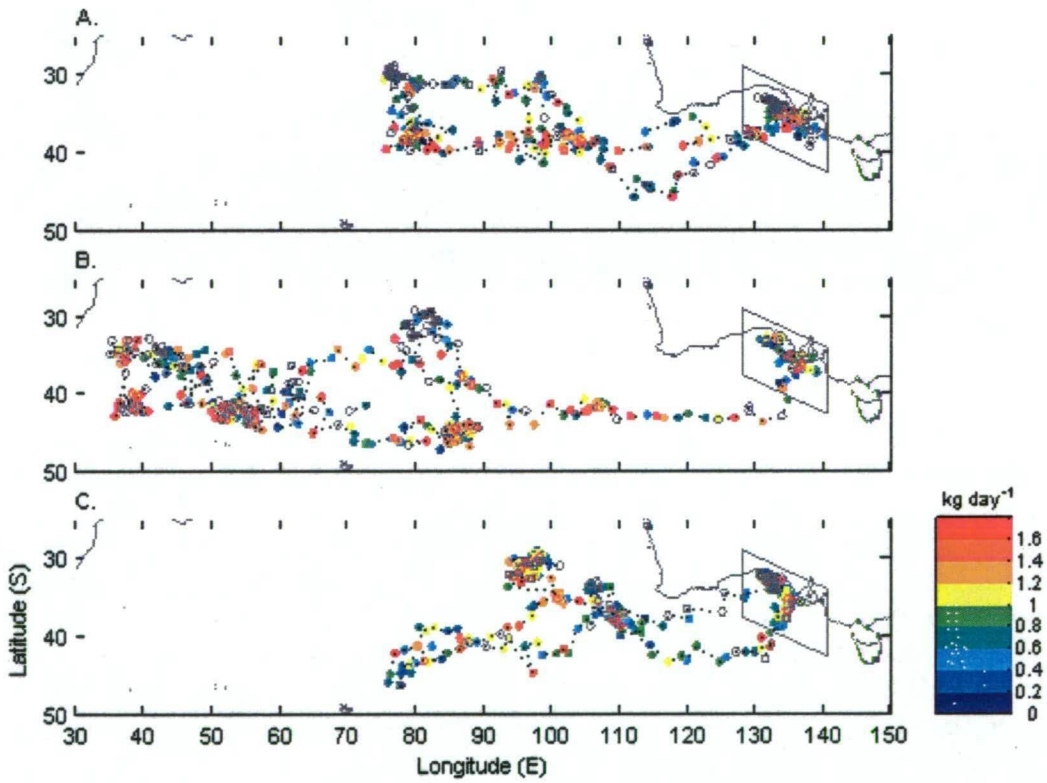

Fig. 4.4. Three examples of SBT migratory paths with daily positions coloured according to estimated daily intake (kg day^{-1}). Open grey circles indicate no feed events occurred. Tracks of (a) SBT97721 for the period 4 February 1998 to 5 December 1998; (b) SBT97731 for the period 12 March 1999 to 1 July 2000; (c) SBT99267 for the period 23 February 2000 to 7 February 2001. The Great Australia Bight region is shown by the grey polygon.

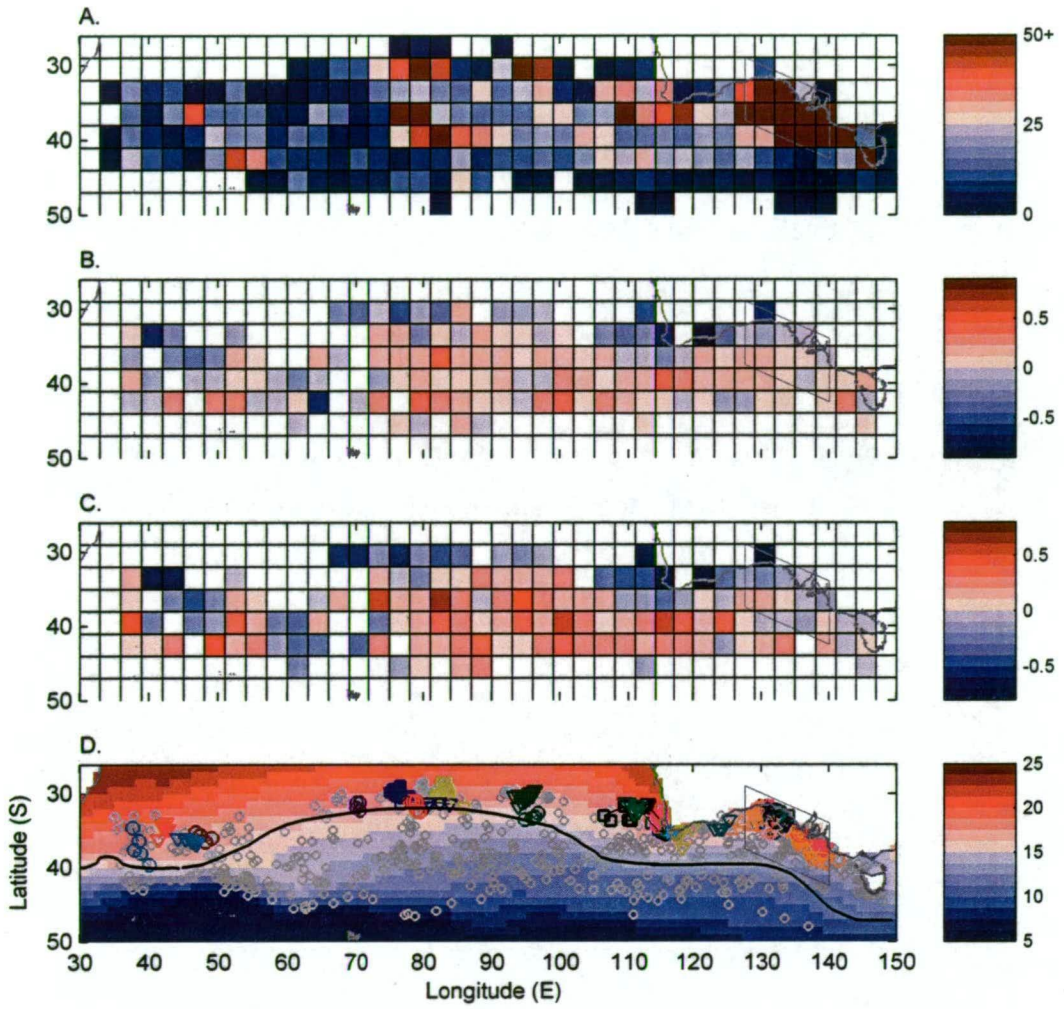

Fig. 4.5. Residency and feeding of juvenile SBT in the south Indian Ocean. (a) Occupancy (days), (b) feeding frequency (feeds day^{-1}), (c) daily intake (kg day^{-1}), and (d) all extended fasting periods of 5 days or more. Panels (b) and (c) are shown as anomalies about the overall mean (0.92 feeds day^{-1} and 0.81 kg day^{-1} respectively) and exclude squares with less than 7 days data. Data are aggregated by 3° squares across fishes (N = 19, n = 5222). In panel (d) colours identify individual fish (N = 17), and symbols link daily positions within a particular fasting period (n = 428 days over 54 separate periods). For example the dark blue represents SBT97721, with the triangles near [83°E, 30°S] showing a 6-day fast in July 1998, and the squares near [78°E, 30°S] showing a 22-day fast in late August 1998, respectively. Grey circles show all other daily positions where non-feeding was recorded. Background shows the 1998–2000 winter-spring SST (°C) climatology (compiled from Jun-Nov monthly NOAA OI SST V2 data, http://www.cdc.noaa.gov/cdc/data.noaa.oisst.v2.html). The climatological position of the northern Subtropical Front (Belkin & Gordon 1996) is also shown for reference (black line).

From the data aggregated across fishes, the relationship between the number of successful and unsuccessful feeding days per square and the total number of days per square was determined to be significantly positive at only two of the six scales investigated (the 5 x 5° grid and 7 x 7° grid, Table 4.4; $|z| > 3$, $P \leq 0.001$). The bootstrap procedure showed significance at these two scales in only 52.9% and 59.2% of the bootstrap samples respectively ($\alpha = 0.01$). Therefore at all scales the bootstrapped parameters were non-significant *i.e.* the confidence intervals for all the parameter estimates straddled zero (Table 4.4).

However, the mixed models revealed significant patterns at the level of the individual fish. At all scales except one, the preferred model contained both a random effect (intercept) for the individual fish and a random effect (slope) for time spent within a square (all LR > 7.9, $P \leq 0.005$, Table 4.5), the single exception being at the 5 degree grid scale (LR = 3.7, $P = 0.05$). The further addition of time as a fixed effect was not supported at any scale (all $|z| < 1.7$, all $P \geq 0.09$). Examination of the model predictions showed opposing effects amongst individual fish: some fish increased feeding probability with time spent in a square, whereas other fish decreased and some showed no effect of time (Fig. 4.6). These patterns were observed consistently over the scales investigated. The significant fish-to-fish variability in the patterns of feeding success over the time spent within an area explains why a population-level parameterization failed to reveal any significant pattern.

The negative relationships relate to prolonged periods of non-feeding observed in some fish. While non-feeding days accounted for 24.0% of all days (Table 4.1), of these 30.5% were actually associated with extended fasts of between 5 and 24 days ($n = 428$ days over 54 periods, $N = 17$ of the 19 fish). These fasting periods occurred throughout the year, within the GAB region during both the first (35.2% fasts, $N = 13$ fish) and the second (24.1% fasts, $N = 5$ fish) summer residencies, as well as within the wider South Indian Ocean (40.7% fasts, $N = 11$ fish). Fasting periods occurred almost exclusively within warmer waters (99.5% of fasting days occurred in waters with daily mean SST > 15°C). The distribution of these periods therefore tended to be along the northern edge of the migratory range observed in this study (Fig. 4.5d). Furthermore, from the position

data available (≥ 5 days, $n = 41$ of the 54 periods) the majority of fasting periods were clustered along relatively tortuous portions of the migratory paths (87.8% had a Linearity Index < 0.5, LI = net movement/total path length during the fasting period) rather than along relatively straight sections of track (Figs 4.4 and 4.5d) *i.e.* coincident with periods of apparent residency.

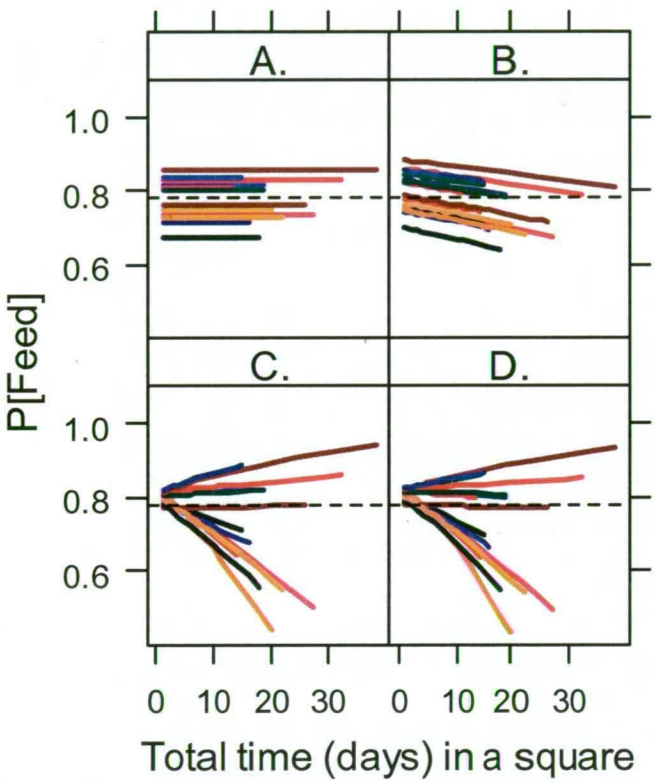

Fig. 4.6. Predictions from generalized linear mixed models (GLMMs) on feeding success/failure in relation to time (days) spent within a grid square. Shown are (a) the base case model with a population mean intercept (dashed line) plus random effects for each fish (coloured lines); (b) as for (a) plus a fixed effect for time; (c) the preferred model with random effects in both the intercept and linear time term, with no fixed effect for time; and (d) as for (c) plus a fixed effect for time. The results are shown for the 3 x 3° grid scale but the patterns were consistent across the scales investigated.

Table 4.4. Results of generalised linear models (GLMs) fit to binomial feeding data at different spatial grids (2 x 2 to 10 x 10 degree squares). Results from bootstrapping across fishes (n = 10000 samples) also shown.

	Binomial GLM								Bootstrap results					
Grid	*df*	Deviance	LL	AIC	Est.	SE	*z*	Pr(>|z|)	Est.	SD	CI		% *P* values[†]	
Size							value				lower	upper	<0.05	<0.01
2	412	825.63	-709.51	1423.02	-0.25	0.21	-1.21	0.23	-0.22	0.48	-1.18	0.76	43.2	30.6
3	191	449.11	-417.43	838.87	-0.78	0.5	-1.56	0.12	-0.62	1.18	-2.74	1.79	58.1	46.5
4	118	360.38	-327.89	659.78	0.75	0.44	1.71	0.09	0.62	0.96	-1.2	2.48	54.3	42.2
5	80	297.75	-267.62	539.23	1.26	0.39	3.22	0.001	0.76	0.86	-1.07	2.35	63.3	52.9
6	60	241.87	-221.75	447.5	-0.12	0.39	-0.3	0.76	-0.11	1	-1.85	1.95	56.5	44.8
7	47	203.98	-186.69	377.38	1.06	0.28	3.79	0.00015	0.76	0.65	-0.59	1.93	69.7	59.2
10	25	131.15	-124.98	253.97	0.03	0.22	0.15	0.88	-0.01	0.47	-1.01	0.78	40.7	27.2

[†] Based on a Chi-squared test.

Table 4.5. Results for generalized linear mixed models (GLMMs) on feeding success/failure in relation to time (days) spent within a grid square.

Grid			Fixed effect β_1			Fixed effects $\beta_1 + \beta_2 t_{ij}$				
size	n	Random effects	LL	LR	$P^{\dagger}$	LL	Est.	SE	z	P
2	1308	$b_{i,1}$	-965.3 [a]			-965.3 [b]	0.0009	0.003	0.282	0.778
		$b_{i,1} + b_{i,2}t_{ij}$	-954.1 [c]	22.43	<0.0001	-954.1 [d]	-0.0006	0.007	-0.094	0.925
3	728	$b_{i,1}$	-554.4			-551.2	-0.015	0.006	-2.522	0.012
		$b_{i,1} + b_{i,2}t_{ij}$	-532.8	43.33	<0.0001	-531.5	-0.023	0.014	-1.694	0.09
4	538	$b_{i,1}$	-479.8			-479.3	0.004	0.005	0.91	0.363
		$b_{i,1} + b_{i,2}t_{ij}$	-470.1	19.37	<0.0001	-470.1	0	0.01	-0.008	0.994
5	397	$b_{i,1}$	-388.2			-388.1	0.001	0.004	0.245	0.807
		$b_{i,1} + b_{i,2}t_{ij}$	-386.3	3.74	0.053	-386.3	0.002	0.006	0.277	0.782
6	345	$b_{i,1}$	-367.3			-365.4	-0.007	0.004	-1.895	0.058
		$b_{i,1} + b_{i,2}t_{ij}$	-356.5	21.51	<0.0001	-356.2	-0.005	0.007	-0.776	0.438
7	284	$b_{i,1}$	-322.4			-5326*	-0.001	0.005	-0.3	0.764
		$b_{i,1} + b_{i,2}t_{ij}$	-309	26.75	<0.0001	-5458*	-0.001	0.013	-0.11	0.912
10	191	$b_{i,1}$	-232.6			-3674*	0.001	0.004	0.231	0.817
		$b_{i,1} + b_{i,2}t_{ij}$	-228.6	7.98	0.005	-3706*	0.001	0.01	0.095	0.924

[a] base model includes a fixed effect for the population intercept (β_1) and random effects ($b_{i,1}$) in the intercept for each ith fish plus errors modelled as a random normal variable $\varepsilon_{ij} \sim N(0, \sigma^2)$; [b] as for (a) plus the linear time (t) per jth square term $\beta_2 t_{ij}$ as a fixed effect; [c] as for (a) plus random effects ($b_{i,2}t_{i,j}$) in the linear time term for each fish; [d] as for (c) plus the linear time term as a fixed effect; [†] The P-value is based on the likelihood ratio (LR) test statistic of model (a) versus model (c) having a χ^2_1 distribution although this may be conservative (Pinheiro & Bates 2000); * These models failed to estimate a reasonable dispersion parameter.

DISCUSSION

Seasonal long-distance migrations are thought to be related to resource distribution, but data on feeding success needed to test this presumption has been difficult to obtain for highly migratory marine species. This is the first study to relate a quantitative analysis of feeding frequency to the foraging ecology of a wild migratory fish. The feeding data are consistent with a predominantly visual generalist predator using adaptive foraging strategies in a seasonally variable environment. However, the combined feeding and movement data do not support the hypothesis that activity is concentrated only in areas where resources are more available thereby increasing feeding success. Instead the data show relatively consistent feeding throughout most of their migratory range, but also highlight previously undocumented non-feeding periods. Given that an animal has an incomplete knowledge of their environment, this may reflect variability in foraging success due to poor predator search strategy, or a poor prey field. Alternatively, these results may indicate that other factors can motivate residency. In light of the rapidly increasing emphasis on telemetry-based studies of mobile marine animals, our results demonstrate the importance of obtaining independent information on feeding when interpreting habitat utilisation from individual animal tracks.

The tagging procedure was designed to minimise handling stress and involved minor surgery, with fish returned to the water less than 2 minutes after landing. Short-term recoveries have established that the surgical wound can completely heal after two weeks. Nevertheless, the majority of fish (68%) took more than two weeks to re-establish normal feeding behaviour after tagging. This post-surgery period was excluded from all analyses, and we believe it unlikely that the tag might have influenced observed patterns in feeding. Although this possibility cannot be excluded, the long-term nature of the archival tag records (some in excess of 40 months) in combination with the high tag-return rates (including recaptures after more than 9 years at liberty) suggest SBT do fully recover from the stress of handling and surgery.

Temporal feeding patterns

The temporal patterns in feeding in relation to time of day and moon-phase are consistent with tunas being primarily visual predators (Itoh *et al.* 2003b; Kitagawa *et al.* 2004). The predominance of dawn feeding had previously been inferred for SBT from stomach fullness as well as fishery targeting strategies (Young *et al.* 1997). Increased activity and enhanced feeding during crepuscular hours has been widely reported across aquatic and terrestrial taxa (Reebs 2002; Kronfeld-Schor & Dayan 2003) and may be due to a combination of factors. For example, vertically migrant prey have not yet descended (Hays 2003) and/or there is a predatory advantage during changing light conditions. Many marine predators also exhibit changes in behaviour over the lunar cycle (Horning & Trillmich 1999) which is further thought to correlate with light-driven changes in the vertical migration of prey.

Further conclusions about the influence of time of day are limited by the subjectivity involved in identifying the separate ingestion of multiple prey items. Using our current methods it is likely that a number of individual meals are identified as a single feeding 'event', and we cannot distinguish between 1 kg ingested in minutes and 1 kg eaten over a number of hours. Distinct multiple feeding events were identified (12.7 ± 4.4 % days, range = 7.0–22.3%) and are probably underestimated, although this may be more important in coastal regions where the main prey are thought to be schooling fish (Young *et al.* 1997). The relatively long duration of each event, similar to the findings from previous studies (Gunn *et al.* 2001; Itoh *et al.* 2003b), reflects the physiological nature of the data. The time-scale for an event (~18h) is comparable to the time to gastric evacuation (Olson & Boggs 1986). However, the daily intake estimates, although only intended as a relative measure, provide very plausible values (Olson & Boggs 1986) for a daily ration of 3.8 ± 0.5 % (range: 2.9–4.9%) of body mass per day[4]. Therefore, our results may in part represent the efficiency of a predator

[4] Based on the length to weight conversion $W = 3.13088L^{2.9058} \times 10^{-5}$ (Robins, 1963).

aiming to fill its stomach once per day, and feeding rapidly to satiation when the opportunity arises.

Seasonal foraging ecology

Our findings show juvenile SBT predominantly exploit the epipelagic ocean (10–150 m), with some feeding also occurring within the mesopelagic layer (> 150 m) particularly during winter. The deepest recorded feeding event (672 m) also provides evidence SBT occasionally forage at very low light levels, consistent with previous reports of deep-sea crustaceans and bottom-dwelling fish in their diet. A deeper winter vertical distribution, and by inference feeding depth, has been previously reported for other tunas (*Thunnus orientalis*, Kitagawa *et al.* 2004) and predatory fish (*Oncorhynchus tshawytscha*, Hinke *et al.* 2005a). Studies of marine predators in the southern oceans such as penguins and seals have also reported deeper diving patterns, increased diving effort, expanded foraging ranges and an increased diversity of prey items during winter (*Aptenodytes patagonicus*, Cherel, Ridoux & Rodhouse 1996b; *Arctocephalus tropicalis*, Beauplet *et al.* 2004; *Eudyptes chrysolophus*, Green *et al.* 2005). Such behavioural flexibility, as observed across a variety of top predators, has widely been interpreted as a response to seasonally reduced epipelagic prey availability and density, ensuring broader diets and higher feeding rates.

Linking feeding and residency

Increasingly, quantitative analyses aimed at elucidating foraging strategies are being applied to high-precision movement tracks such as obtained via Global Positioning System collars (Morales *et al.* 2004). However, the large errors associated with geolocation methods, and to a lesser extent Argos satellite estimates, present substantial limitations to the application of such track-based analytical methods (Bradshaw, Sims & Hays 2007). The geographical grid scales examined in this study, although somewhat of an artificial imposition, were selected to cover an appropriate range given both the coarse resolution of the data and the spatial scales of the movements being studied. The range also encompassed scales previously identified as characteristic of mesoscale foraging

patches for other top predators operating over similar spatial scales, although shorter timescales (Fauchald & Tveraa 2006).

Our analysis found time spent within an area had no clear relationship with feeding success. Most interestingly, this was primarily a result of the high degree of individual variation with both positive and negative trends observed between individuals. Importantly, these patterns were observed consistently across all the spatial scales examined. This finding provides strong evidence against the interpretation of high-use areas for migratory species, commonly determined from only horizontal and/or vertical movement data in the absence of any independent information on feeding activity, as successful feeding grounds (Robinson *et al.* 2007). This strengthens previous findings from studies using indirect measures such as body condition (Bailleul *et al.* 2007) and mass gain (Bradshaw *et al.* 2004b) which found equivocal or no evidence for a relationship between foraging success and spatial usage of areas. Explanations for the observed variation in trends can be (1) time spent within an area is more likely to be a measure of searching activity rather than a direct proxy for foraging success, given that predators have imperfect knowledge of their environment; and (2) predators do not necessarily feed all the time, and may spend time within areas for alternative reasons.

Although animal movements may be driven by resource distribution, superimposed on this is the fact that they may have incomplete knowledge of their environment, particularly in heterogeneous marine environments. At very broad geographical and seasonal scales, predators may have an awareness of prey distribution (Bradshaw *et al.* 2004b; Houghton *et al.* 2006), and at fine-scales foraging is likely to be dominated by proximal sensory clues (Sims & Quayle 1998). However, the mesoscale search strategies by which animals locate prey remains a pivotal problem in ecology. To examine whether animals use optimal search strategies recent studies have used empirical data on both horizontal and vertical movements (Edwards *et al.* 2007; Sims *et al.* 2008), as well as simulations (Sims *et al.* 2006). Our finding that juvenile SBT did not consistently spend longest where their feeding success was highest may reflect that as juveniles some individuals have poor search strategies (Sims *et al.* 2006); however no

information on adult foraging is currently available to determine if this is a specific juvenile behaviour. Since our study examined same-age individuals within a narrow size range, therefore presumably similar levels of foraging experience and skill, the high variability in patterns of feeding between individuals are not expected to be related to age or size. Yet as unsexed juveniles it was not possible to determine whether the differences were sex-related.

The variable patterns of feeding success may reflect real differences in the availability of prey or the prey type targeted by individuals. High individual variability in feeding behaviour, not specific to juvenile cases, has been reported in many other top predators including seals (*Halichoerus grypus*, Austin *et al.* 2006a), albatross (*Diomedea exulans*, Weimerskirch *et al.* 1997) and penguins (*A. patagonicus*, Putz & Bost 1994), and generally attributed to the patchy and unpredictable prey distribution. It is also a possibility that the high spatial overlap in the locations of poor feeding success are indicative of a relatively poor season(s) within a region of usually predictably high forage (Bradshaw *et al.* 2004b). Future studies should reveal if (1) SBT do show fidelity to particular regions and (2) the identified areas of low feeding success are consistent or variable between years.

The second explanation for the observed variation in feeding trends is that large predators do not necessarily feed all the time, and may spend time in particular areas for alternative reasons. Particularly in coastal waters, where SBT exhibit strong schooling behaviour, movements may be driven by social factors rather than individual-based decision making (Gunn & Block 2001). In an oceanic context, association with floating objects and/or topographic structures has been proposed as a behaviour that increases the encounter rate between isolated migratory fishes (Freon & Dagorn 2000). Alternatively, particular topographic features may be important for other reasons such as resting or for navigational reference (Castro, Santiago & Santana-Ortega 2001). Movements may also be related to predator avoidance, which is often ignored for large species but has been demonstrated in bottlenose dolphins (*Tursiops aduncus*) and green turtles (*Chelonia mydas*) where there are high abundances of sharks (Heithaus & Dill 2006; Heithaus *et al.* 2007). Finally, it has been suggested that when tunas forage

within frontal zones, the warm side of fronts may be used as a thermal refuge, enabling them to feed in cold waters while minimising the cost of staying warm (Gunn & Young 1999; Kitagawa *et al.* 2004). Thermal conditions are known to play a driving role in the large-scale movements of a range of marine predators including turtles, fish and mammals (McMahon & Hays 2006; Neat & Righton 2007). In our study the prevalence of non-feeding periods in warm waters (Fig. 4.5d) provides some evidence that resting periods may occur within thermal refuges over longer timescales (of days to weeks) in the south Indian Ocean.

In summary, we have shown the value of integrating direct information on feeding when interpreting habitat utilisation from individual animal tracks. Our findings do not show a straightforward relationship between feeding and residency. Current efforts to develop novel methods for determining feeding activity on a wide range of marine species will continue to advance our understanding of foraging ecology and the critical linkages between animal behaviour, movement, environment and energetics.

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5. Predictors of feeding success in a wild migratory fish: integrating telemetry, environmental data and modelling techniques

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ABSTRACT

Foraging theory predicts that mobile predators should target high profitability areas with plentiful resources and minimise time spent moving between these areas. This has led to a focus in recent literature on the identification of "hotspots" important for migratory marine predators, *i.e.* regions where predators spend disproportionate amounts of time ostensibly due to high prey abundance; and determination of the environmental features characteristic of such areas. Here, we investigate the factors predictive of foraging success in a wild migratory fish, southern bluefin tuna (SBT, *Thunnus maccoyii*), by integrating telemetry-based feeding and movement data with environmental data using statistical modelling techniques. The results show increased feeding and predictability of feeding occurs in the coastal waters of southern Australia, providing some evidence that this area represents a fixed foraging "hotspot" for juvenile tuna during the austral summer. However, in the open ocean bluefin did not fit the common model of migration, but rather showed a pattern of relatively high foraging success throughout their migratory range, especially during periods of continuous travel. Interestingly, foraging "coldspots" as well as "hotspots" appeared across individual tracks, predicted most strongly by warm ocean temperatures. These results provide a new perspective on the ecology of migration within the context of the heterogeneous ocean environment, where the continuous opportunistic feeding of wide-ranging generalist predators may in fact represent a norm in animal behaviour.

Key words: *migration; top predators; foraging ecology; feeding success; tuna*

Chapter 5

INTRODUCTION

The phenomenon of animal migration was described by Dingle (1996) as a persistent and directed movement from one habitat to another. For mature individuals seasonal movements are often associated with travel to breeding sites, but in immature or non-breeding animals seasonal migrations are often motivated by seasonal cycles in food supply (Alerstam *et al.* 2003). In terms of foraging theory, individuals are predicted to exploit high profitability areas with plentiful resources and minimise time spent moving between these areas (Stephens & Krebs 1986). Yet in heterogeneous environments prey may be patchily distributed in space and time (Boyd 1996). This is particularly true for marine environments where the distribution of food resources generally reflects the heterogeneity of physical features and associated biological productivity (Sims *et al.* 2008). Recent literature has focused on identifying "hotspots" for migratory marine predators, areas of presumably abundant prey, and determining the environmental characteristics of these areas (Sydeman *et al.* 2006) particularly in order to identify regions that may warrant special status as conservation areas, for example as critical foraging habitat (Block *et al.* 2003; Hooker & Gerber 2004).

Obtaining direct information on feeding in long-ranging, deep-diving marine species has long presented a major challenge (Biuw *et al.* 2007). Telemetry developments over the past 20 years (Cooke *et al.* 2004) have led most studies to analyse patterns in movement and/or behaviour as indirect proxies for foraging (Fauchald & Tveraa 2003; Jonsen, Myers & Flemming 2003). Short-term measurements of feeding have been obtained for a number of sea birds and mammals from sensors measuring stomach temperature, oesophageal temperature, mouth-opening events or echo-location buzzes (Austin *et al.* 2006b; Watwood *et al.* 2006). Uniquely, in temperate tunas the physiological response to feeding has a distinctive signature pattern of visceral warming that is measurable by a temperature sensor surgically implanted within the body cavity (Carey *et al.* 1984; Gunn *et al.* 2001). This provides an accurate long-term record of when feeding occurs for wild fishes (Bestley *et al.* 2008) and bypasses the need to infer foraging indirectly from patterns in movement or behaviour. This study found an apparent

disconnection between feeding and movement with no clear relationship observed between feeding success and time spent within an area (Bestley *et al.* 2008).

Direct observation of the relative degree of feeding enables the foraging success of a migratory marine predator to be directly and quantitatively linked to the physical characteristics of its' natural environment. Foraging success is ultimately a function of (1) the spatial and temporal distribution of biological productivity, and (2) the ability of predators to locate and exploit these resources. In marine environments biological productivity is often concentrated in coastal/shelf waters and around other bathymetric or oceanographic features such as upwelling zones, frontal features, or sea-ice margins (Mann & Lazier 2005). However, information on prey abundance and distribution is usually unavailable especially for long-ranging species. Yet since environmental characteristics are important determinants of the distribution of prey resources, they are also expected to be an important influence on predator foraging success. Therefore, there is an increasing effort to integrate biological and physical information from electronic tags with oceanographic data, for example from satellites. Various physical characteristics such as temperature and ocean colour (from which phytoplankton concentration can be estimated) are increasingly being examined as predictors of the distribution and behaviour of apex marine predators (Bradshaw *et al.* 2004a; Pinaud & Weimerskirch 2005; Suryan *et al.* 2006). Quantifying the direct relationship between feeding and environmental influences can provide important insight into the specific timing and spatial patterns of migratory movements and importantly, enable broader prediction of where predators are expected to go and to forage successfully. These empirical findings can further be used more broadly to inform models of predator-prey interactions (Lima 2002; Ford *et al.* 2007) or ecosystem structure and functioning including the role of transient top-predators (Boyd & Murray 2001).

The physical characterization of feeding habitats remains challenging due to both the complexity of the natural environment and the nature of the telemetry data. Biologging studies, widely applied throughout terrestrial and marine systems, provide large volumes of detailed information collected through time, usually from relatively few individuals. The hierarchical (nested within

individuals) and time-series structure of the data violate statistical assumptions of independence which underpin most traditional analytical methods (Venables & Ripley 2002). To properly interpret this data therefore represents a non-trivial challenge which has limited our ability to fulfil the ecological objective of most studies, that is to draw inferences at the population level. Consequently, the development of appropriate statistical methods is an active research area. The implementation of techniques such as mixed-effect models (Pinheiro & Bates 2000), which provide a more flexible and robust treatment of within- and between-individual variation than traditional repeated measures models, has been aided by the increase in computing capabilities over recent years. However there remains much scope for development, particularly for example in the practical treatment of the time-series. In this paper, we provide a method that models a full categorical (feed/no feed) time-series, obtained from telemetry data collected by wild tuna, as a Markov process. This explicitly accounts for the non-independence in the data, and demonstrates how valuable ecological insight can in fact be obtained from quantifying both the nature of the time-dependence and the effect of individuals.

Therefore in this study we analyse long-term feeding data recorded by archival tags deployed on juvenile southern bluefin tuna throughout their coastal summer residency and oceanic migration cycle. This species provides a unique opportunity for studying the links between environmental variability, feeding and movement for a highly migratory marine predator at an ocean-basin scale. We provide an appropriate statistical method to model feeding as a time-dependent process. The models integrate data on ocean temperature collected by the tags, data on oceanic productivity collected by satellites, and a number of other environmental covariates with the aim of determining what environmental characteristics are predictive of high foraging success. Our approach further enables the evaluation of whether apparent "hotspot" areas of high use are important areas of enhanced foraging success.

METHODS

Markov chain analysis of feeding success

While telemetry has long provided the tools for collecting detailed information on individual behaviour, analytical methods appropriate for time-series data are relatively recently being applied in this field (Jonsen *et al.* 2003; Patterson *et al.* 2008). Most current applications involve movement data and models for analysis of feeding probability (Franke *et al.* 2006) are comparatively rare. Given the ecological and biological processes involved, *e.g.* prey patchiness, digestion, it should be reasonable to treat feeding as a time-dependent process where the probability of feeding is to some extent dependent on yesterdays' influence. We chose to model feeding as a Markov process, where the probability of feeding at the next time step (t) is a function of the current and past feeding states. While 1st-order Markov processes only depend on the current state, higher-order processes incorporate dependencies at greater time lags. To analyse a predators' feeding success, let S_t be a random state variable that may take on two values

$$S_t = s_t \in \{F, \overline{F}\}$$

where F denotes a feed having occurred, and $\overline{F}$ denotes no feed. We seek to determine the probability $P(S_t = s_t \mid s_{t-1})$ which can be modelled as a function of one or more covariates X_t

$$logit(P(S_t = s_t)) = \begin{cases} \alpha_{0,F} + \alpha_{1,F} X_t, & s_{t-1} = F \\ \alpha_{0,\overline{F}} + \alpha_{1,\overline{F}} X_t, & s_{t-1} = \overline{F} \end{cases}$$

The likelihood Λ_t of the t^{th} data point can be written

$$\Lambda_t = P(S_t = F)\mathrm{I}(s_t = F)[1 - P(S_t = F)]\mathrm{I}(s_t = \overline{F})$$

Here I(.) is the indicator function, *i.e.* I =1, $\rightarrow s_t = F$ (feed) and I = 0, $\rightarrow s_t = \overline{F}$ (no feed). Another way to view this is by

$$\Lambda_t = P^{\mathrm{I}(s_t=F)}(1-P)^{1-\mathrm{I}(s_t=\bar{F})}$$
$$= \left[\frac{P}{1-P}\right]^{1-\mathrm{I}(s_t=F)}(1-P)$$
$$\log\Lambda_t = \mathrm{I}(s_t = F)\mathrm{logit}(P_t) + \log(1-P)$$

Therefore the Maximum Likelihood Estimate (MLE) for the model is simply $\prod_t \log\Lambda_t$. To examine whether a 1st-order Markov process is appropriate we can compare a 1st and 2nd-order Markov model. In the 2nd order case, ideally within the full model with all covariates considered, we would fit $P(s_t = F_t \mid s_{t-1}, s_{t-2})$. Diagnostics for comparing the Markov models are described in Appendix C.

Model development and selection

In developing the models we employed both standard generalised linear models (GLMs) and generalised linear mixed models (GLMMs) using a binomial distribution for feeding success. Mixed models are particularly suited to nested data collected on individuals, and both can be formulated as Markov chains to account for temporal correlation in the data. This is done by simply including as a predictor the observation(s) of whether a feed was observed to occur from up to the *n*th time-steps) prior. For example, in a 2nd order Markov chain the current state is influenced by both the previous state and the one prior to that *i.e.* at both *t*-1 and *t*-2.

To obtain an initial idea of the shape of relationships between feeding success and the environmental predictor variables, we first considered a relatively full generalized additive mixed model (GAMM) with all environmental covariates included and also simple GAMMs fitted separately to each covariate. Based on the outcomes we then fit (A) GLMs, and (B) GLMMs with individual fish included as a fixed and random effect respectively. Since interactions between continuous variables may not be meaningful in a model, and may be very difficult to interpret in any case, only interactions between continuous and factor variables were considered. The fish interaction terms identified in the GLMs were then used to inform appropriate other random effects terms in the GLMMs. Model selection

for the GLMs proceeded via automatic stepwise selection using Akaike's Information Criteria (AIC). For the GLMMs, model selection was also determined via AIC, starting from a full model with fixed effects retained only if they improved the fit (ΔAIC > 2). Likelihood ratio tests were also performed. Diagnostics for assessing model fit are described in Appendix C. All analyses were carried out using R-software v2.5.1 (R Development Core Team, 2007), the GLMMs fitted in the package lme4 v0.99875-7 (Bates 2007) and the GAMMs in mgcv v1.3-25 (Wood 2006).

Feeding and movement data

Juvenile SBT (n = 200) were caught by pole-and-line in 1998–2000 during their annual austral summer residencies within the Great Australia Bight (GAB). Archival tags (model Mk7, Wildlife Computers, Redmond, WA) were surgically implanted into the peritoneal cavity ventral to the stomach, and programmed to sample pressure (depth), ambient light, ambient water temperature and visceral temperature every 4 minutes. From 51 recaptures, long-term data (*i.e.* > 120 days) were recovered from 29 tags. Daily longitudes, determined using light-based geolocation methods (Hill 1994), showed long-distance migrations into oceanic waters during winter-spring (Bestley *et al.* 2008). This study focuses on the 19 age-3 animals (LCF = 99 ± 3 cm, range = 93–111 cm, Eveson *et al.* 2004) which migrated west into the south Indian Ocean (longitudinal range = 35–147°E). Latitudinal estimates, problematic via light-based methods, were determined by comparing the surface water temperature recorded by the tag with satellite SST estimates (Teo *et al.* 2004; Bestley *et al.* 2008). The pattern of visceral warming associated with digestion was used to detect feeding events and estimate relative intake size following procedures outlined previously (Gunn *et al.* 2001; Bestley *et al.* 2008). To link an individual's feeding success with the resolution of its movement path the data were examined as a daily time-series (Fig. 5.1). As multiple feeding events were not often identified (12.7 ± 4.4% of days) the data were treated as binomial.

Environmental predictors

Environmental data examined as potential influences on feeding success are tabulated in Appendix A. Sea surface temperature (SST) calculated from the tag data was examined to determine whether a preferred range was evident, and the standard deviation of the mean SST included as an indicator of local variability. Remotely-sensed surface chlorophyll-a concentration (SSC) was included as an indication of biological productivity. To provide a relative as well as an absolute estimate of production we also included the SSC anomaly relative to climatology. Lunar illumination was calculated using standard astronomical equations. Day of year was included to capture any seasonal trends not represented within the environmental covariates considered. In case of strong interannual trends release year was included as a factor, although the number of fish per year was small (n = 10 in 1998, n = 4 for 1999 and n = 5 for 2000). Longitude was examined for broad spatial trends. Finally, although spatial boundaries in a fluid environment are always somewhat artificial, we expected the influences operating within the coastal waters of the GAB could differ substantially from those in the open ocean. Hence, we included a factor variable of whether the daily position fell within or outside the region described by the coordinates: 127.5°E, 29°S; 127.5°E, 37.5°S; 140°E, 42.5°S; 140°E, 34°S (Fig. 5.1).

More tortuous paths are generally presumed to be indicative of searching or foraging behaviour, whereas a persistent directionality in movement trajectories is generally associated with travel (Bovet & Benhamou 1991). To incorporate some information on an individual's movement strategy we calculated a simple linearity index (straight line distance/total path length) as an indication of whether a path was more linear (values close to 1) or more tortuous (values close to 0). For the time-series of each individual this was calculated over a moving 7-day window, selected to match the temporal scaling of the other environmental covariates.

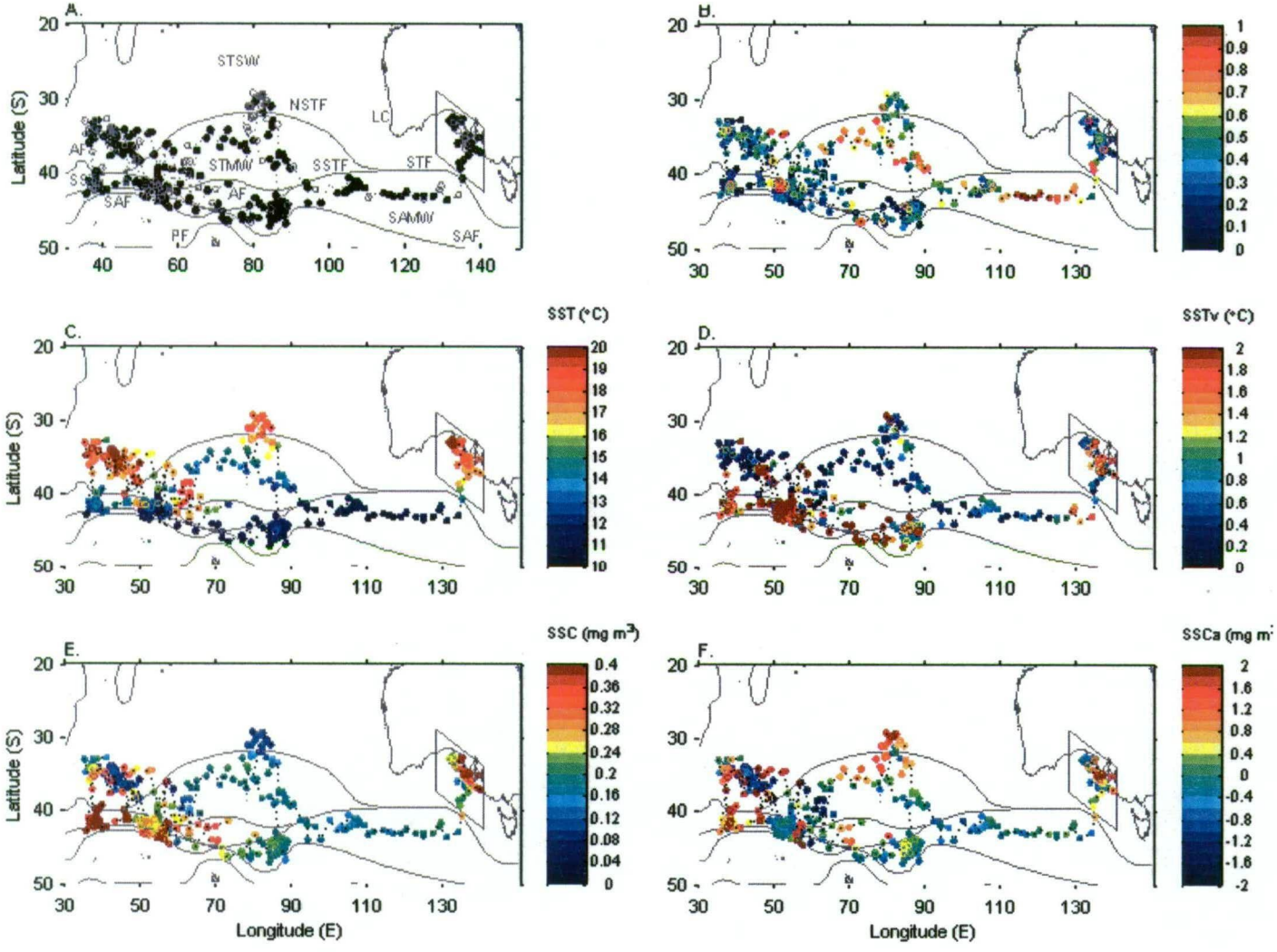

Fig. 5.1. Example migration path of an individual bluefin (97731) with daily positions coloured by (a) binary feeding success: feed (black), no feed (grey), (b) linearity index of movement (0: tortuous, 1: straight line), (c) sea surface temperature (SST, °C), (d) sea surface temperature variability (SSTv, °C), (e) sea surface colour (SSC, mg m^{-3}), and (f) sea surface colour anomaly (SSCa, mg m^{-3}). The GAB region is shown by the grey polygon. The climatological positions of the major fronts (Belkin & Gordon, 1996) are also shown for reference (grey lines): LC – Leeuwin Current; STSW – Subtropical surface water; STF – Subtropical front, and its north (NSTF) and south (SSTF) components; AF – Agulhas front; SAF – Subantarctic front; PF – Polar front; STMW – Subtropical Mode Water; SAMW – Subantarctic Mode Water.

RESULTS

The 19 juvenile fish collected data for periods of 141 to 496 days (mean ± SD = 327 ± 95 d, n = 6221 total). The period immediately following the tagging surgery and prior to recommencement of normal feeding lasted between 5 and 38 days, and these data were excluded from all analyses (leaving n = 5859 d total). Light-based longitude estimates and SST data from the tag were available for 97.1% of days and SST-based latitudes then determinable for 89.1%. The final data included in the models, having complete movement and environmental covariates, represented 86.0% of days *(i.e.* n = 5041 total). These data span the period 26 January 1998 to 7 February 2001, with the data available for individual fish ranging between 104 and 422 days. The GAB region contained 42.6% of this data (range: 9.7–79.8% per fish). Feeding events were recorded on 77.1% of all days (range: 67.4–86.0% per fish).

An example of the environmental conditions occurring over the geographic range of the bluefin migrations is shown in Fig. 5.1. The warm waters of the Great Australia Bight had generally low surface chlorophyll during midsummer, increasing later in the season (Appendix A, Fig. A1). The Subtropical and Subantarctic Mode water regions were areas of cool, stable temperatures, with moderately low surface chlorophyll levels (~0.16 mg m^{-3}). The warmer waters north of the North Subtropical Front mostly showed low absolute values of surface chlorophyll, however these generally represented a seasonal (austral winter) high and therefore positive chlorophyll anomalies. The Agulhas Retroflection in the far western basin, a region of intense mesoscale activity due to the close confluence of three major fronts, was characterized by very high variability in surface temperatures, generally elevated surface chlorophyll, and both positive and negative chlorophyll anomalies (Fig. 5.1). However, only four individuals spent substantial periods of time within this region.

Model selection

The most parsimonious GLM model determined on the basis of the AIC included sea surface temperature (SST) and SST variability (SSTv), sea surface colour

anomaly (SSCa), day of year (DOY) and the linearity index of movement (LI) as significant predictors of daily feeding success (Appendix B, Table B2). Feeding success showed no consistent trend with respect to release year, lunar phase, longitude or mean SSC. Feeding within the coastal GAB habitat showed different trends to the open ocean, with this influential variable creating significant interaction terms with SST, SSCa and whether the animal fed the previous day. Only within the GAB was there a strong increase in predicted success if a feed had occurred the previous day, *i.e.* an animals' feeding (or non-feeding) state was less changeable day-to-day. With respect to ocean temperature, a negative quadratic relationship predicted highest feeding success at intermediate SST (12–17°C) and moderate variability (SSTv ~1°C) (Appendix B, Fig. B1). However a Fish:SST interaction indicated significant variability in this relationship between individuals. The GAB:SSCa interaction showed there was no relationship between SSCa and feeding in the GAB, but in the ocean there was a significant negative quadratic relationship. Reduced success was predicted particularly at high positive anomalies (*e.g.* SSCa > +2), that is high seasonal primary production relative to the normal mean production in an area. The polynomial relationship between feeding and LI was positive, predicting increased feeding during periods of both more tortuous (LI ~ 0.2) and directed (LI > 0.8) movements (Appendix B, Fig. B1).

In relation to day-of-year, lowest feeding success was predicted in early summer with a distinct peak in mid-late summer then a decline to relative stability at ~100 days and for the remainder of the year (Appendix B, Fig. B1). However a Fish:DOY interaction ($df = 90$) was also retained which allowed for great flexibility in modelling the time-series of individual fish. If this term was not included in the original model then longitude, which displays strong collinearity with DOY ($r = 0.54$, Appendix A, Fig. A1), and a Fish:longitude interaction, was retained. In addition SSC which also displays a seasonal trend (Appendix A, Fig. A1), became a significant predictor having a negative relationship with feeding success specifically within the GAB (Appendix B, Table B2).

Taking into account which variables had important interactive effects with individual fish we examined a number of different random effects structures for

the GLMMs (Appendix B, Table B1). The preferred GLMM on the basis of the AIC contained both a random intercept for fish and a random slope for SST. The predictor covariates retained as significant within the final GLMM, and the estimated coefficients, were very similar to the results obtained from the GLM models (Appendix B, Table B2). The only substantive difference was the GLMM model without DOY did not identify longitude as significant.

Model diagnostics

Examination of whether the 1st order Markov assumption was appropriate yielded interesting results. Model selection on the basis of an AIC statistic or an analysis of deviance showed an improved fit if a lag-2 observation (O_{t-2}) was included ($\Delta AIC = 5, \chi^2_1 = 7, P = 0.0075$) *i.e.* the prediction of the current feeding state was informed by whether feeding occurred on the previous day *and* the day before that. However, the addition of the term yielded no substantive change to the model predictions and no improvement in the model diagnostics (Appendix C, Fig. C1). The outcome was similar for the GLMM models. Notably, regardless of whether both O_{t-1} and O_{t-2} were included the diagnostics showed all models to perform more poorly in predicting when the previous observation was a zero (*i.e.* no feed). This may partly reflect the skewed nature of the response variable *i.e.* if all days were predicted as successful feeding the model would be correct more than 75% of the time. Further investigation revealed that strongly false positive predictions, *i.e.* prediction of above-average feeding success where a feed was not in fact observed, constituted 8% of all predictions, whereas strongly false negative predictions constituted only 3% of all predictions (Appendix C, Table C1). While false negatives tended to relate to the SST covariate (94% had SST>16°C), false positives predominantly occurred when a feed had been observed the previous day (91%) *i.e.* indicated it was harder to 'flip out' of a feeding state. These patterns were identical from both the 1st and 2nd order models, therefore we concluded the 1st order Markov model was likely to be sufficient.

The simple goodness of fit measures showed an apparently good concordance between the observed and predicted feeding (Appendix C, Fig. C2). However, inspection of the approximate residuals A_i revealed some problematic

patterns, with the models tending to over-fit both the very high and very low feeding probabilities (Appendix C, Fig. C3). These patterns were largely removed only in the best-fit GLM, which allowed for the highest fish-to-fish flexibility given the fish interaction terms with both DOY and SST (Appendix C, Fig. C2a). Further examination of the residuals did not clearly reveal problems with respect to any other individual covariate (Appendix C, Figs C4 and C5).

Model predictions of feeding success in wild tuna

The time-series of feeding probabilities predicted from the final GLM and GLMM models were similar overall, given the similarities in model structures, although the GLM allowed for more variability between individuals (Fig. 5.2). Mean feeding probabilities of individual fish ranged between 0.67–0.86 in the GLM and between 0.69–0.84 in the GLMM. Successful feeding was generally predicted throughout the observed migratory range (Fig. 5.3). In particular, high feeding success tended to occur along portions of the migratory path that were relatively straight, *i.e.* during periods of directed travel. Periods of reduced feeding success, predicted for most but not all individual fishes, tended to occur amongst clustered locations within the warmer waters of the subtropical south Indian Ocean and coastal Australia, including within the GAB itself (Fig. 5.3). Consequently, feeding indices (calculated as average feeding probability multiplied by estimated average daily intake) were variable between different regions of the South Indian Ocean (Table 5.1). The most profitable feeding region, visited by most individuals and characterised by an elevated feeding probability in combination with a slight increase in intake size, appeared to be within the cooler waters of the central south Indian Ocean (Fig. 5.3, Table 5.1). The subtropical margin, in contrast, represented relatively poor feeding habitat whereas the Agulhas and GAB regions were of intermediate quality.

Table 5.1. Observed and predicted feeding success for wild juvenile SBT in regions of the South Indian Ocean. Results are shown from the best-fit GLM and GLMM models. Data shown as mean (S.D.) across fishes.

	Observed					Predicted		
Region*	Fish			Intake		P(Feed)	Feed Index†	Range
		Days Spent	Proportion Days Fed	(kg)				
Agulhas Retroflection	4	78 (64)	0.76 (0.09)	1.04 (0.21)	GLM	0.78 (0.15)	0.80 (0.09)	0.70–0.90
					GLMM	0.77 (0.07)	0.79 (0.11)	0.65–0.89
Subtropical Indian Ocean	14	36 (30)	0.70 (0.20)	0.87 (0.18)	GLM	0.70 (0.17)	0.62 (0.20)	0.21–0.92
					GLMM	0.71 (0.11)	0.62 (0.17)	0.29–0.84
Central South Indian Ocean	15	35 (21)	0.83 (0.10)	1.26 (0.34)	GLM	0.83 (0.08)	1.03 (0.16)	0.81–1.37
					GLMM	0.85 (0.02)	1.06 (0.28)	0.79–1.95
Great Australia Bight	19	123 (61)	0.77 (0.08)	0.91 (0.13)	GLM	0.78 (0.07)	0.70 (0.08)	0.54–0.82
					GLMM	0.79 (0.08)	0.71 (0.08)	0.55–0.85
All	19	308 (96)	0.76 (0.06)	1.00 (0.10)	GLM	0.78 (0.06)	0.77 (0.04)	0.68–0.85
					GLMM	0.77 (0.05)	0.77 (0.05)	0.68–0.85

* Regions defined as follows: Agulhas Retroflection 40–60°E, 35–45°S; Subtropical Indian Ocean 70–110°E, 30–35°S; Central South Indian Ocean 70–110°E, 37.5–42.5°S; Great Australia Bight see Fig. 5.3 and Methods.

† Feed index calculated as probability of feed multiplied by estimated daily intake

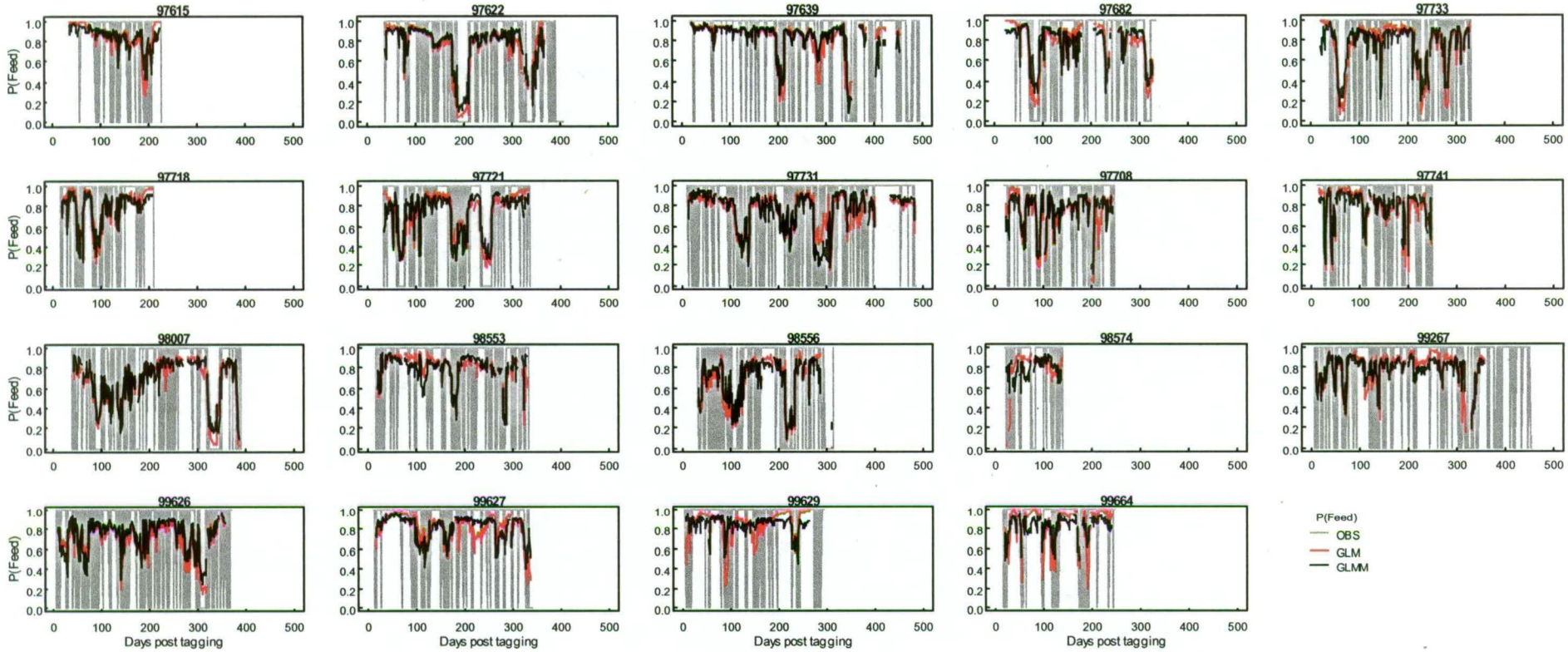

Fig. 5.2. Time-series showing observed (gray: binary 1-feed, 0-no feed) and predicted feeding success for individual juvenile southern bluefin tuna from best-fit models (1) GLM including fish as a fixed effect (red), and (2) GLMM including fish as a random effect (black).

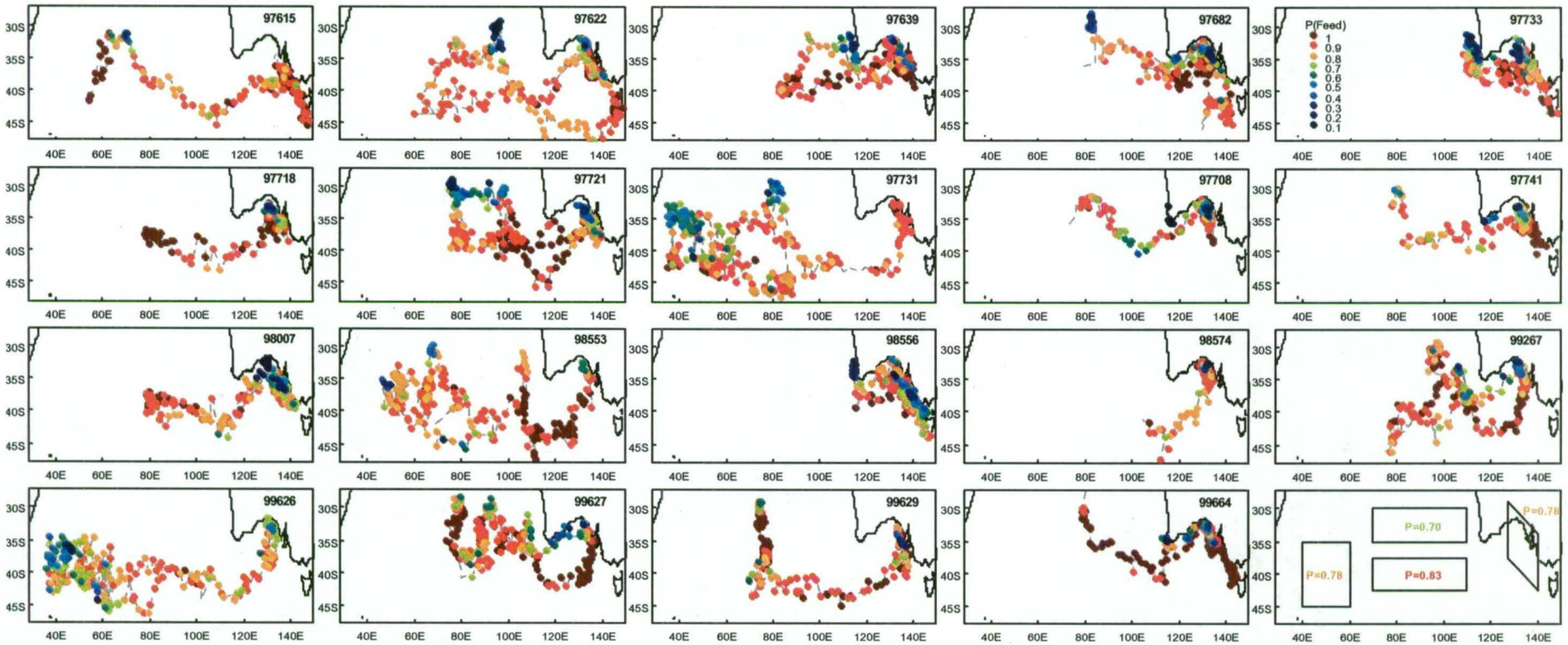

Fig. 5.3. Migration paths of juvenile southern bluefin tuna, with predicted feeding probabilities from the best-fit GLM model indicated by colour. Final panel shows predictions summarised across fishes for four regions (see Table 5.1).

Chapter 5

DISCUSSION

Novel telemetry methods which collect direct information on feeding in wild animals bypass the need to infer foraging indirectly from patterns in horizontal movements or vertical swimming/diving behaviour. In addition, Markov models enable complex time-series data collected by individuals to be modeled within an appropriate framework. Taken together this allows the feeding success of a highly migratory marine predator to be directly linked to the physical characteristics of its' marine environment throughout the course of annual long-distance migrations. The results demonstrate important differences between coastal and oceanic seasonal feeding habitats, and indicate a complex interplay of factors influence feeding success. However, the high feeding success overall, which was not confined to specific areas and included periods of rapid transit, we propose reflects the continuous foraging opportunism of these high-performance 'energy speculators' (Dickson 1995). In contrast, some apparent foraging "coldspots", *i.e.* extended periods spent within areas of low feeding success, within warm water locations challenge the traditional interpretation of residencies. This provides a new perspective on the ecology of migrations which is more complex than the commonly expected strategy of directed non-feeding commuting movements to "hotspot" zones of predictable prey concentrations.

Characteristics of seasonal feeding habitats

The migration path was characterized by two very different environments, coastal and oceanic, providing distinctly different seasonal feeding habitats. First, the models indicate feeding is more predictable within the summertime coastal habitat, that is if a fish feeds one day it is significantly more likely to feed the next. This was not the case for the open ocean environment. Second, from the time-series (DOY) term it appears that following poor initial success in the early summer there is a general elevation in feeding probability during the mid-summer for most, but not necessarily all, individuals. Third, this does not translate into a higher feeding likelihood overall for the coastal habitat as compared with elsewhere. Actually, feeding probabilities are average and the estimated intake sizes appear somewhat smaller (Table 5.1). Fourth, residence times within the

coastal habitat are quite long in comparison to other regions (Table 5.1). Taken together, these components form a picture of the coastal Great Australia Bight as a "hotspot" insofar as it provides a feeding habitat where more predictable, although potentially smaller, feeding opportunities are consistently available over a relatively long period of time. This in turn is consistent with the general idea of migration, *i.e.* that animals move away once the quality diminishes.

These patterns are consistent with what is known of the feeding strategies adopted by bluefin tunas in coastal compared with oceanic environments. In inshore waters, schooling aggregations are formed (Lutcavage & Kraus 1995; Royer *et al.* 2004) which generally prey heavily on shoaling fishes (Young *et al.* 1997; Chase 2002). In offshore waters, their diet comprises a greater diversity of fish, squid and crustaceans (Young *et al.* 1997) indicative of a more opportunistic targeting of less predictable and more dispersed prey items. Analogous predation strategies are consequently adopted by the commercial tuna fisheries, with surface fisheries (purse-seine, and historically pole-and-line and troll gears) exploiting the inshore schooling aggregations and long-line fisheries harvesting dispersed fishes offshore (Caton 1991).

The advantages associated with an annual residency in the coastal waters of the Great Australia Bight may extend beyond the predictability of the prey field. For example, the effort associated with prey capture for schooling predators as compared with individually foraging predators may be lower and reduced daily swim-speeds should result in lower overall metabolic costs. It has also been proposed that the high levels of solar isolation warming the surface layers of the GAB may provide thermal advantages to this endothermic species. Increased aerobic performance (Dickson 1995) and increased biochemical activity (Carey *et al.* 1984) are two benefits of elevated body temperatures, potentially making more energy available for growth during this period (Gunn & Block 2001). The extent to which each of these factors benefits SBT is not known. However analyses of length-distributions indicate growth is fastest during the summer (Eveson *et al.* 2004). Yet during a winter field experiment, caged fish fed to satiation gained condition rather than length (Carter *et al.* 1998) which could be indicative of alternating seasonal growth strategies. Anecdotal evidence from the longline

fishery suggests fish condition (*i.e.* lipid content) is seasonally variable and highest in the cold southerly waters, however direct information on body condition (Willis & Hobday 2008) throughout a season or between seasons needed to investigate these hypotheses is currently lacking.

Feeding during transit

In the open ocean, the predicted feeding success for juvenile SBT was generally high throughout most of their migratory range and furthermore was elevated during periods of directed movement. This finding apparently contradicts the hypothesis that predators use area-restricted search behaviour, characterized by frequent changes in direction, within areas of high feeding profitability and making high-speed directed movements between such areas (Benhamou 1992, but see Bestley *et al.* 2008). This migration model is commonly adopted for species that make a direct transit between breeding sites and specific foraging zones of predictable prey such as frontal zones, shelf edges or sea ice margins, where individuals then spend the majority of their time (Ferraroli *et al.* 2004; Bailleul *et al.* 2007). Area–restricted search is also likely to be an appropriate model for the majority of seabirds which are pause-travel foragers, *i.e.* cannot feed on the wing, and must travel without feeding between patches of suitable prey. Indeed many other marine species whose foraging behaviour involves bouts of diving, surfacing to breathe and subsequent resting periods may also fit a movement model where feeding activity tends to be suppressed during transit (Austin *et al.* 2006b).

A positive association between feeding and straight-line movements is however consistent with what would be expected from animals using an extensive search behaviour, efficient for finding highly dispersed prey items or isolated patches of prey (Hill, Burrows & Hughes 2002; Sims *et al.* 2006). Such a movement pattern has been described for the wandering albatross, and interpreted as a response to the highly scattered distribution of their squid prey, made possible by low travelling costs over long distances (Weimerskirch *et al.* 2005). Extensive wandering movements and continuous foraging has also recently been reported for leatherback turtles searching for dispersed gelatinous zooplankton (Hays *et al.*

2006), with these movements in some cases being assisted by large drifts with ocean currents (Luschi *et al.* 2006). The successful feeding displayed during transit in combination with the extended periods of residency in the open ocean may indicate SBT use multiple strategies, and be more evidence for the flexibility of tuna foraging behaviours.

The interplay between cause and effect in the SBT migratory patterns remains somewhat speculative. For example, it may be that individuals move rapidly along preferred migratory routes, and need to supply elevated energetic requirements during these migratory periods; the result is a feeding pattern which resembles a successful extensive search mode. Alternately, the directed movements may in fact be driven by a highly dispersed prey field and be overlaid on the need to reach plentiful prey patches eventually. Many marine species adopt efficient search strategies to scan vast volumes and effectively exploit prey resources when encountered (Sims *et al.* 2008), and tunas and billfishes in particular possess remarkable physiological adaptations for both efficient and rapid swimming and food processing (Dickson 1995). Therefore, in either case the pattern of successful feeding during travel is perhaps an expected result of the evolution of these migratory, opportunistic predators. This novel data highlights a pattern of feeding migrations that may be more common in marine species, particularly predatory large pelagic fishes, than is currently documented.

Environmental predictors of feeding

Some individual SBT displayed periods of both very high and very low feeding success during periods of less directed, more residential movements. Warm ocean temperatures were generally predictive of lower feeding success, a finding consistent with previous observations (Bestley *et al.* 2008). The additional strong negative influence of high variability in surface temperatures may have been linked the good feeding success which generally occurred within the more stable cool waters of the central South Indian Ocean. The expectation of elevated feeding along frontal features, often demarcated by sharp temperature changes or variability, does not seem to be supported by this finding. However, any influence

of fine-scale features (Sims & Quayle 1998) would be masked by the coarse temporal and spatial scale of this study.

The seasonal elevation in surface chlorophyll, which occurs predominantly along the warm northern margin of the migratory range, was also negatively associated with feeding success in the open ocean. The feeding index calculated for this region was consequently very low, indicating a foraging "coldspot" (Table 5.1). This is a somewhat counter-intuitive result given the widespread expectation of enhanced feeding opportunities associated with enhanced plankton biomass and biological productivity. Yet although representing a seasonal (austral winter) maxima, and relief of the oligotrophic conditions typical in subtropical waters (Machu & Garcon 2001), the absolute levels of surface phytoplankton in the area remained relatively low compared with elsewhere (Fig. 5.1). However, our study also highlighted the significant variability between fishes in relation to temperature, and showed some individuals did successfully forage within the warm waters of the subtropical margin (Fig. 5.3). These results therefore do not yet provide conclusive evidence for whether SBT spend time within this region for foraging purposes or for other reasons *e.g.* for navigation, as a thermal refuge or simply resting periods (Bestley *et al.* 2008).

Determining linkages between animal movement, environmental conditions and feeding success presents some substantial challenges which are highlighted by this study. Environmental variables are often correlated, not necessarily linearly, and so a variety of statistical interactions can be expected. Moreover, feeding patterns of a top predator will only be weakly correlated to the majority of these imperfect predictors. Feeding is of course probably driven by the abundance and type of prey field encountered by an individual. However direct measurements of prey distribution, where they rarely exist, usually represent a spatially and temporally restricted fraction of a migratory species' range. Developing model-based real-time estimates of prey fields is therefore an approach currently being widely investigated (*e.g.* Lehodey, Chai & Hampton 2003). These issues are manifested in our models – for example, the uptake of the time-varying SSC and longitude terms in place of the day-of-year term. Whether increased phytoplankton densities actually negatively influence feeding in the

coastal habitat, for example by reducing water clarity and impairing visibility (Brill *et al.* 2002), or whether the trend of declining feeding late in the season simply occurs collinearly with changes in SSC, is debatable. In our opinion the importance of the highly flexible DOY term in differentiating trends for individuals highlights (i) that individual fish are different, but also (ii) that we are likely to be lacking some important predictor variables which may help to discriminate those differences.

Modelling individual variability

Our analysis revealed consistent responses by individual animals to most environmental variables. However, important individual-level effects were linked to both temperature and day-of-year. Furthermore, comparison of the two approaches, modelling individual effects as either fixed or random terms, revealed these differences were not sufficiently well captured by the mixed models. The random effects terms provided less flexibility and consequently over-fitted influences identified as important for most, but not all, individuals. As discussed above, this could be a consequence of the present study lacking important predictor variables *e.g.* on the specific prey field available within a given temperature regime. However, the relatively small number of individuals in this study may also be a factor. The escalation in wildlife telemetry studies is now resulting in very large datasets collected by an ever growing number of individual animals. For the inference of population-level trends from these data, a more sophisticated modelling approach than allowing an extra model parameter per animal is needed, so a mixed-modelling approach is certainly preferable. However it is equally important to adequately account for real variability across individuals, which appears as a persistent feature emerging across studies and species. In many cases this may be adequately addressed by a careful investigation of where the variability lies, for example through exploration of different random effect parameterizations. However in many instances it may also require a more thoughtful collection of data on the factors expected to be directly responsible for the observed patterns and variability, not often a straightforward task in studies of dynamic open ocean systems.

Conclusions

Feeding is the result of an animals' response to a variety of factors including physiological constraints, environmental influences, prey dynamics and social behaviour. Increasingly, bio-logging studies are being used to identify "hotspot" regions for marine predators. Our results highlight the value of obtaining direct information on foraging success when developing interpretations of habitat use. Furthermore, our results illustrate the value of integrating telemetry-based data with other sources of information within an appropriate modelling framework when developing predictions of what constitutes good feeding habitat. This study forms one step in the ongoing development of more sophisticated and useful analytical approaches that we hope will help ecologists get the most from their hard-earned telemetry data-sets. Studies adopting such an approach can both test and generate hypotheses about foraging models and ultimately the motivations and determinants of animal migration.

ACKNOWLEDGEMENTS

Many thanks to M. Basson and M. Bravington for advice on statistical methods.

APPENDICES

Appendix A. Covariates considered as predictors of feeding success

Table A1. Table of covariates considered as predictors of daily feeding success for juvenile southern bluefin tuna. To obtain some idea of the shape of relationships between feeding success and the environmental variables a full general additive mixed model with all covariates was explored and also simple GAMMs fitted separately to each covariate.

Covariates	Type	Form	Description
Fish	Factor (19)		ID number for each of 19 individual fish. Fit as a fixed effect in the GLM models and a random effect in the GLMM models
Previous observation	Factor (2)		Fish fed (1) or did not feed (0) on the day prior, formulates the Markov chain
Environmental variables			
Sea surface temperature average (SST)	Continuous	Quadratic	Mean ambient water temperature in the surface 5m* as measured during a 24hr period by the external temperature sensor on the archival tag
SST standard deviation (SSTv)	Continuous	Quadratic	Standard deviation of the mean ambient water temperature in the surface 5m as measured during a 24hr period by the external sensor on the archival tag. Values were square-root transformed†.
Sea surface colour average (SSC)	Continuous	Quadratic	Average surface chlorophyll-a concentration (in mg m^{-3}) from the SeaWIFS 8-day 9km resolution product. Calculated for an area 2° longitude x 3° latitude centred on the daily geolocation estimate to take into account the geolocation errors (Teo *et al.* 2004). Values were log-transformed†.
SSC anomaly (SSCa)	Continuous	Quadratic	Anomaly of the average SSC value relative to the climatology. The climatological mean was calculated from the 8-day composites over the 5-year period September 1997 – September 2002, and subtracted from the mean SSC value. This was then standardized by the standard deviation of the climatological time-series, a normalization which reduces the influence of variance from any one location.
Lunar phase	Continuous	Linear	The illuminated fraction of the disc of the moon for a given day ranging between 0 and 1
Day of year (DOY)	Continuous	5^{th} order polynomial	Day of year ranging between 1 and 365
Longitude	Continuous	3^{rd} order polynomial	Decimal degrees ranging between 35.1E and 148.7E

GAB	Factor (2)		Daily geolocation estimate located within (1) or outside (0) the GAB region bounded by the area (127.5E, 29S), (127.5E, 37.5S), (140E, 42.5S), (140E, 34S)
Release year	Factor (3)		Release year of an individual (1998: n = 10, 1999: n = 4, 2000: n = 5) was included in case of strong interannual trends
Movement metrics			
Linearity Index (LI)	Continuous	3rd order polynomial	Linearity of movement (LI) calculated as the straight line distance (SLD) divided by the total path length (PL), *i.e.* LI = SLD/PL, based on daily geolocation estimates for each individual fish over a 7-day window. Values range between 0 (tortuous) and 1 (straight line).

* Each tag had been previously checked for depth drift and a linear correction applied where necessary using standard zero offset correction techniques. †All variables were visually examined using normal probability plots, and due to a strong right-skew (*i.e.* clustering at lower values) average SSC and SST variability were both transformed.

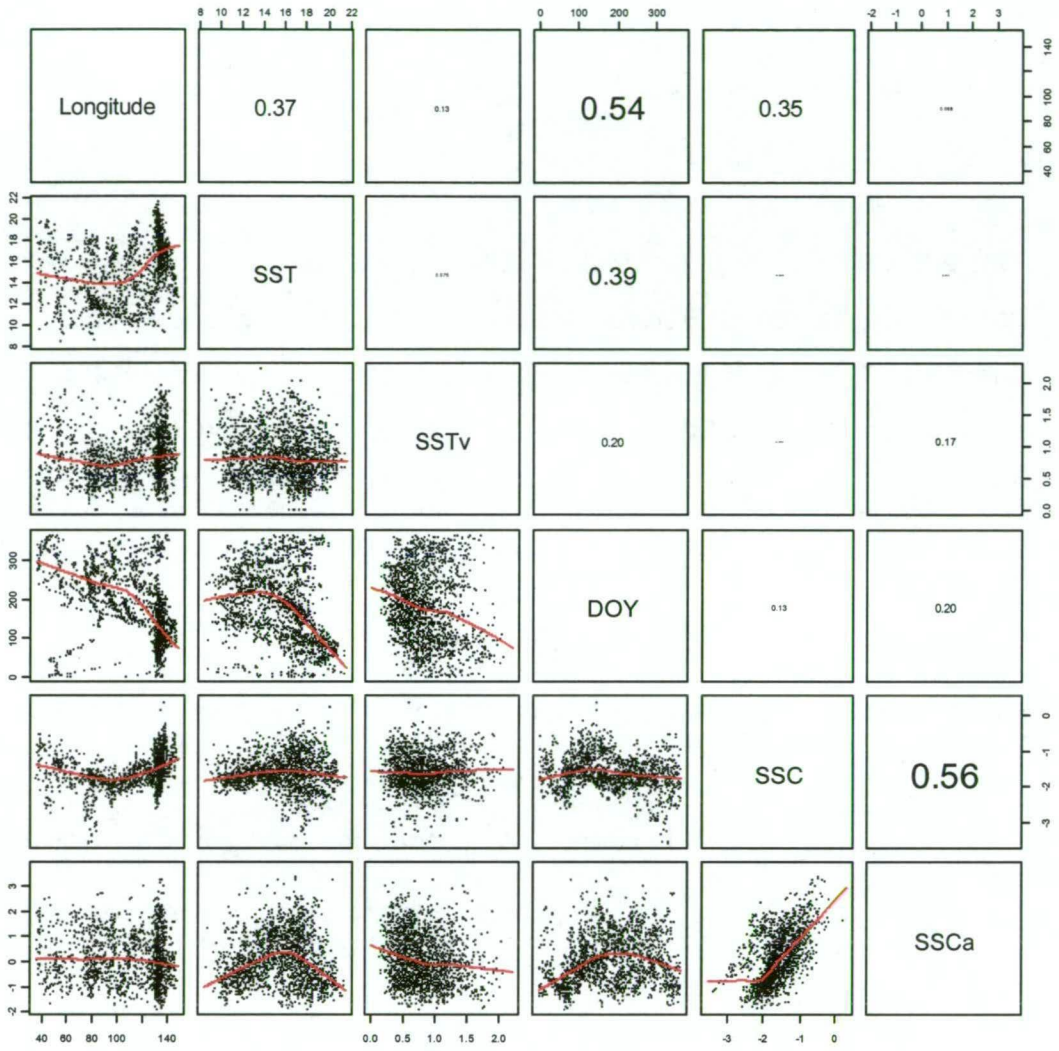

Fig. A1. Correlation between environmental predictor variables. Spearman's *rho* statistic is used to estimate a rank-based measure of association. Red line is a LOWESS smoother which uses locally-weighted polynomial regression.

Appendix B. Model selection

Table B1. Results of the determination of the optimal structure of the random effects for GLMM models. Includes the degrees of freedom (*df*), Akaike's Information Criteria (AIC), Bayesian Information Criteria (BIC), log likelihood (LL), deviance and delta AIC (ΔAIC). Best fitting model structure is given in bold print.

Random effect*	*df*	AIC	BIC	LL	Deviance	ΔAIC
Fish	35	4787.57	5015.96	-2358.79	4717.57	29.22
Fish + linear SST	**37**	**4758.35**	**4999.79**	**-2342.17**	**4684.35**	**0**
Fish + quadratic SST	40	4760.60	5021.61	-2340.30	4680.60	2.25
Fish + linear DOY	37	4783.14	5024.58	-2354.57	4709.14	24.79
Fish + linear SST + linear DOY	38	4757.99	5005.96	-2341.00	4681.99	-0.35
Fish + quadratic DOY	non-convergence					
Fish + 3rd order DOY	44	4784.11	5071.22	-2348.05	4696.11	25.76
Fish + 4th order DOY	49	4789.89	5109.63	-2345.95	4691.89	31.54
Fish + 5th order DOY	55	4794.06	5152.95	-2342.03	4684.06	35.71
Fish + GAB	37	4779.52	5020.96	-2352.76	4705.52	21.18
Fish + linear LON	32	4822.73	5031.54	-2379.36	4758.73	64.38
Fish + quadratic LON	35	4821.52	5049.90	-2375.76	4751.52	63.17
Fish + 3rd order LON	39	4827.22	5081.70	-2374.61	4749.22	68.87

* All models were fitted with the full fixed effects structure *i.e.* all the explanatory variables and interactions considered.

Table B2. Environmental predictors of feeding success for southern bluefin tuna from the best-fit GLM and GLMM models. Results shown as parameter estimate β (S.E.). 95% Highest Posterior Density intervals are also given for the GLMM parameter estimates (MCMC sample of $n = 10000$). Models including and excluding the day of year (DOY) term are both shown. GLMM random effects include a random intercept term for fish (σ_f) plus a linear random slope term for SST (σ_{sst}).

	With DOY term			Without DOY term		
	GLM [a]	GLMM [b]		GLM [a]	GLMM [b]	
Random effects						
σ_f		0.38			0.37	
σ_{sst}		20.10			21.40	
Predictors	β (S.E.)	β (S.E.)	95% CI	β (S.E.)	β (S.E.)	95% CI
GAB1 [c]	1.05 (0.28)	0.76 (0.20)	0.40 – 1.21	0.90 (0.30)	0.76 (0.20)	0.37 – 1.18
GAB0	-0.02 (0.21)	0.11 (0.20)	-0.34 – 0.48	-0.02 (0.22)	-0.04 (0.21)	-0.46 – 0.37
OBS.Prev1	0.90 (0.12)***	0.84 (0.13) ***	0.60 – 1.08	1.05 (0.12)***	0.97 (0.12) ***	0.75 – 1.22
SST	-29.53 (15.66)^	-4.53 (15.65)	-40.78 – 24.44	-10.00 (15.23)	8.60 (15.65)	-20.13 – 43.65
SST^2	-49.29 (8.58)*** †	-64.35 (8.61) ***	-81.28 – -46.16	-37.59 (8.33) ***†	-50.46 (8.52) ***	-69.29 – -35.24
SSTv	-2.53 (3.14)	-1.75 (3.15)	-8.40 – 4.22	4.30 (2.82)	5.06 (2.81)^	-0.54 – 10.57
$SSTv^2$	-21.35 (2.65)***	-21.52 (2.65) ***	-26.60 – -16.51	-18.76 (2.58) ***	-18.57 (2.57) ***	-23.92 – -13.77
SSC				-20.52 (8.09)*	-21.33 (8.31)*	-38.01 – -5.18
SSC^2				9.28 (6.12)	11.09 (6.35)^	-1.20 – 23.81
SSCa	-1.44 (4.89)	-4.20 (5.00)	-14.34 – 4.82	-1.49 (7.21)	-3.76 (7.36)	-19.83 – 8.79
$SSCa^2$	6.98 (3.79)^	8.24 (3.86)"	0.92 – 15.85	3.47 (4.27)	4.12 (4.32)	-4.36 – 12.96
LI	-1.68 (2.81)	-2.18 (2.82)	-7.79 – 3.20	-1.86 (2.82)	-2.69 (2.80)	-8.44 – 2.62
LI^2	0.06 (2.70)	0.08 (2.71)	-5.09 – 5.43	-0.19 (2.67)	0.02 (2.69)	-5.51 – 5.00
LI^3	9.43 (2.67)**	9.68 (2.70)**	4.55 – 15.19	9.78 (2.64)**	9.99 (2.68)**	4.97 – 15.38
DOY	-15.62 (4.00) ***	-15.63 (3.98) ***	-23.35 – -7.88	NA	NA	
DOY^2	15.61 (3.80)***	13.47 (3.75)**	5.99 – 20.71	NA	NA	NA
DOY^3	3.03 (3.00)	2.34 (3.00)	-3.03 – 8.73	NA	NA	NA
DOY^4	-18.64 (2.88)***	-16.74 (2.94) ***	-22.27 – -10.90	NA	NA	NA

Table B2 Cont.

Predictors	β (S.E.)	β (S.E.)	95% CI	β (S.E.)	β (S.E.)	95% CI
DOY[5]	12.51 (2.91)***[†]	14.14 (2.94) ***	8.13 – 19.85	NA	NA	NA
LON				3.82 (5.28)		
LON^2				6.30 (4.44)		
LON^3				-0.57 (2.94)[†]		
Interactions						
GAB0:OBS.Prev0	-0.86 (0.17)***	-0.82 (0.17) ***	-1.16 – -0.48	-0.99 (0.17) ***	-0.94 (0.17) ***	-1.26 – -0.61
GAB0:SST	-41.48 (16.12)*	-69.71 (15.67) ***	-97.77 – -32.14	-62.46 (16.42) ***	-83.31 (16.01) ***	-118.00 – -54.82
GAB0:SST^2	9.46 (9.98)	21.31 (9.93)"	-0.63 – 39.93	-3.22 (9.85)	7.37 (9.84)	-10.54 – 28.78
GAB0:SSC				16.57 (10.16)^[††]	23.02 (9.64)"	3.38 – 42.10
GAB0:SSC^2				-6.57 (7.29)	-6.55 (7.42)	-21.65 – 7.59
GAB0:SSCa	-4.49 (6.28)	-3.31 (6.38)	-14.99 – 9.84	-2.41 (8.59)	-3.88 (8.52)	-19.28 – 13.97
GAB0:SSCa^2	-19.94 (5.38)**	-20.19 (5.40)**	-31.27 – -10.21	-15.59 (5.81)*	-16.09 (5.84)*	-27.59 – -4.65

[a] GLM model selection by automatic stepwise AIC procedure. Final AIC's are 4706 and 4770 respectively for models with and without DOY term. Parameter estimates for fish terms not shown.

[b] GLMM model selection by stepwise deletion of least significant terms. Final AIC's are 4744 and 4787 respectively for models with and without DOY term.

[c] The reference level is within the GAB

^ ≤0.10; " ≤0.05; * ≤0.01; ** ≤0.001; *** ≤0.0001 denotes P-values from the z-distribution

[†] For comparison of main terms the fish interaction terms were deleted from the best-fit GLMs; [††] indicates term significance becomes P ≤0.001 ** in full model with all interactions.

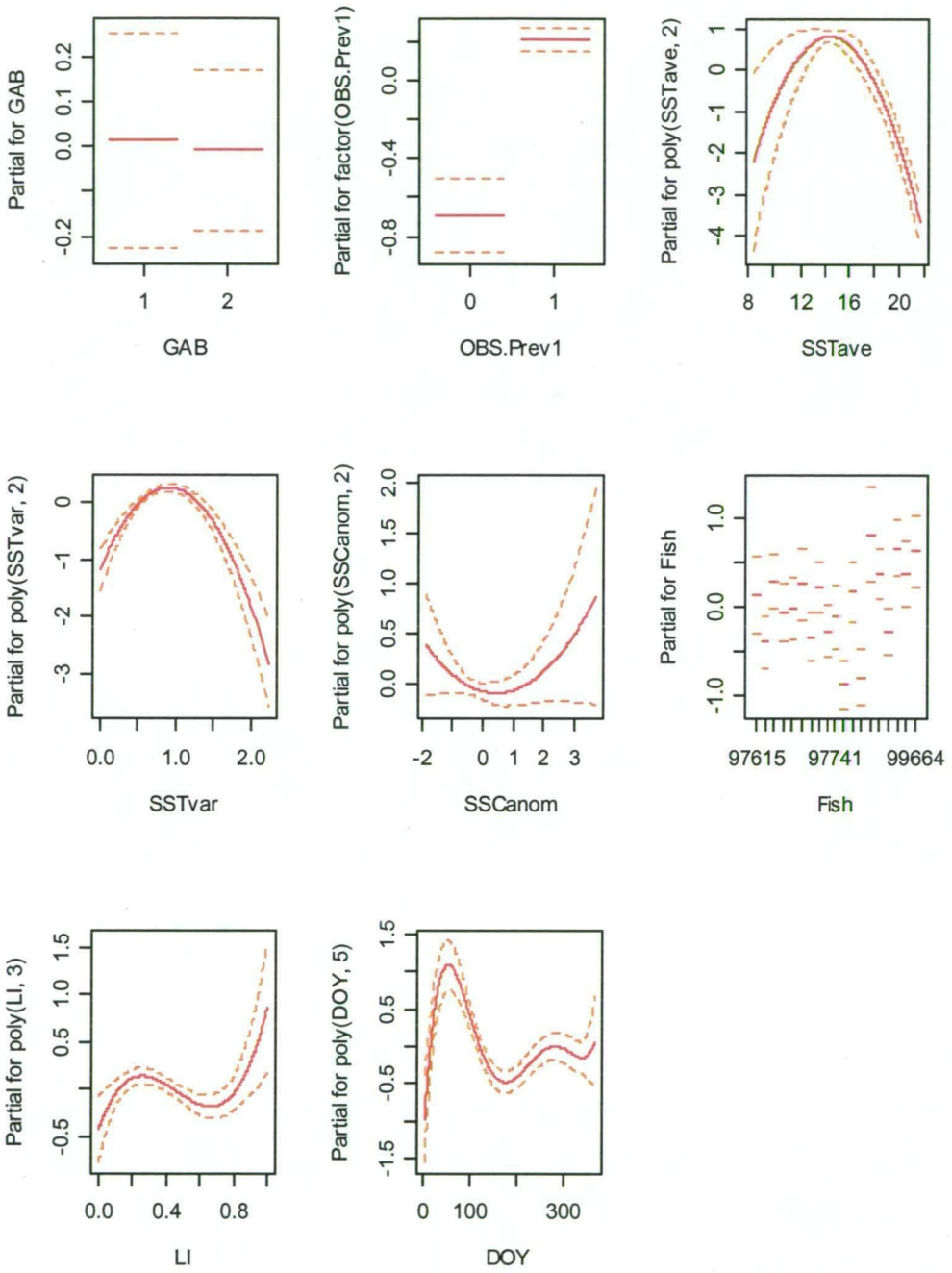

Fig. B1. Partial plot of predictors for the best-fit generalized linear model. For visualization of the effects of main terms the two fish term interactions (*i.e.* Fish:poly(SST,2) and Fish:poly(DOY,5) were omitted.

Appendix C. Model diagnostics

(1) Markov assumption. It is possible that the models continue to accept prior feeding observations from t-1, t-2 … t-n days prior. To examine the effect of leaving out a given predictor covariate on the outcome, we can adopt the following procedure. Define

$$A_t = \log\left\{P_t^{O_t}(1-P_t)^{1-O_t}\right\}$$

where at time t, P_t is the predicted probability and O_t is the corresponding data point of whether a feed was observed or not. Taking the sums

$$\sum_t A_t \mathrm{I}(O_{t-n} = F) \text{ and } \sum_t A_t \mathrm{I}(O_{t-n} = \overline{F})$$

gives an indication of whether the particular covariate (in this case an observation O_{t-n}, n time-steps prior) is influential on the predictions and should have been included in the model.

(2) Model fit. Developing appropriate diagnostics of model fit for binomial (non-proportional) data is not straightforward. A simple method to inspect the goodness of fit is to divide the range of possible predicted (fitted) probabilities into equally sized bins, and to compare for each bin the mean expected proportion of successes with the observed proportion of successes for the data points falling into that bin. However, this method equally weights all bins, regardless of how much of the data is represented in each. Another approach for a more appropriate diagnostic is to categorize the predicted probabilities and for each category i, over all observations j, calculate

$$\sum_j P_{ij} = n_i \overline{P}_i$$
$$\sum_j O_{ij} = O_i$$

where n_i is the number of, and $\overline{P}_i$ is the mean of, the predicted probabilities falling in that bin categorized so that all $n_i\overline{P}_i$ are approximately equal, and O are the coinciding observations. Under our model, we expect that

$$E(O_i)' = n_i\overline{P}_i$$
$$v(O_i)' = n_i\overline{P}_i(1-\overline{P}_i)$$

so examine as an approximate residual

$$A_i = \frac{O_i - n_i\overline{P}_i}{\sqrt{n_i\overline{P}_i(1-\overline{P}_i)}}$$

which should be ~$N(0,1)$. The same process can be repeated, categorising by each covariate to examine whether the model displays any irregularities with respect to any particular covariate.

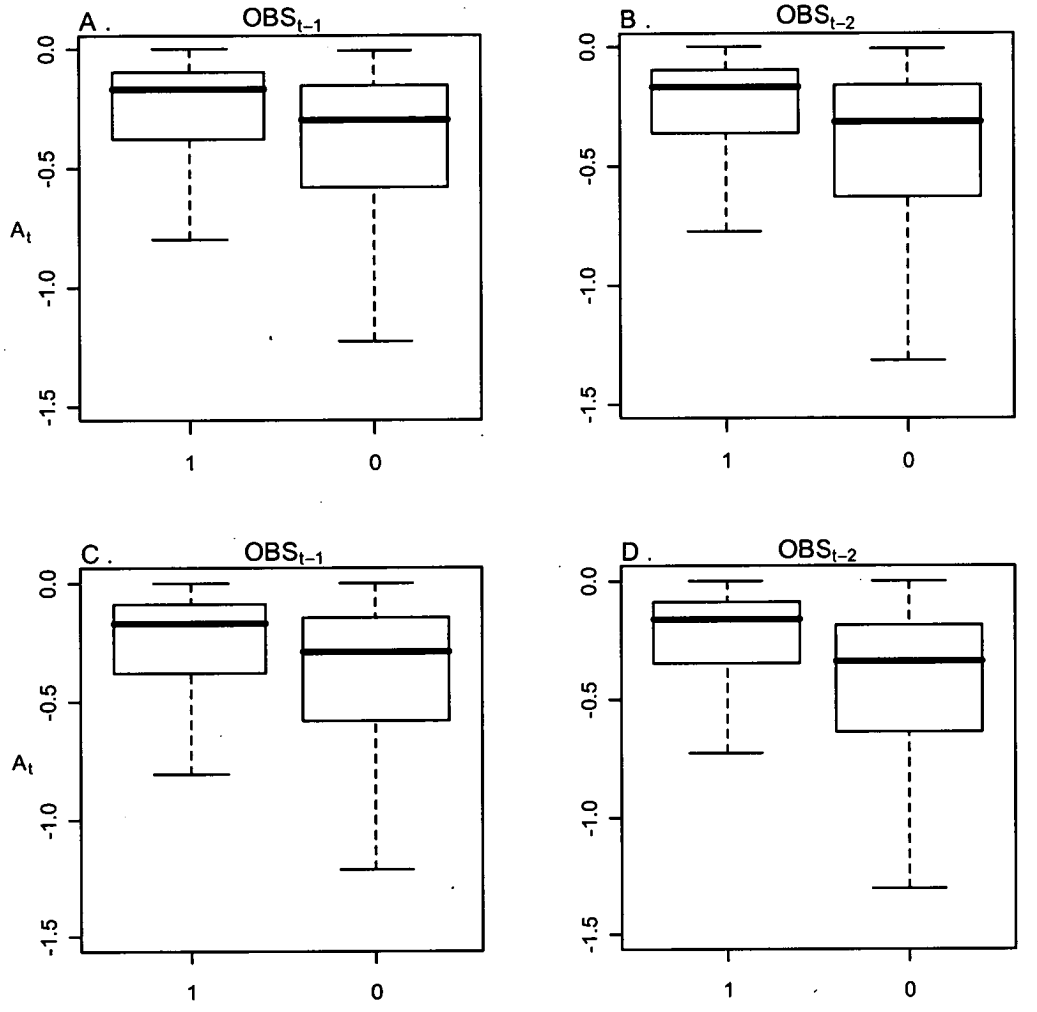

Fig. C1. Diagnostic plots examining the 1st order Markov assumption. Results for the diagnostic statistic $A_t = \log\left\{\hat{p}_t^{\,o_t}\left(1-\hat{p}_t\right)^{1-o_t}\right\}$ are shown for the best-fit GLM which includes OBS_{t-1} (A) but not OBS_{t-2} (B). Secondly, the same results are shown (C and D) for the same model fitted with both OBS_{t-1} and OBS_{t-2} included.

Table C1. Observed and predicted feeding probabilities. Results are shown for the best-fit GLM, from which the mean overall predicted feeding probability across fishes is $P = 0.78$ (Table 1).

Observed	Predicted probabilities		
	Low ($P<0.5$)	Intermediate ($0.5 \leq P < 0.78$)	High ($P \geq 0.78$)
No Feed	0.08	0.07	0.08
Feed	0.03	0.16	0.58

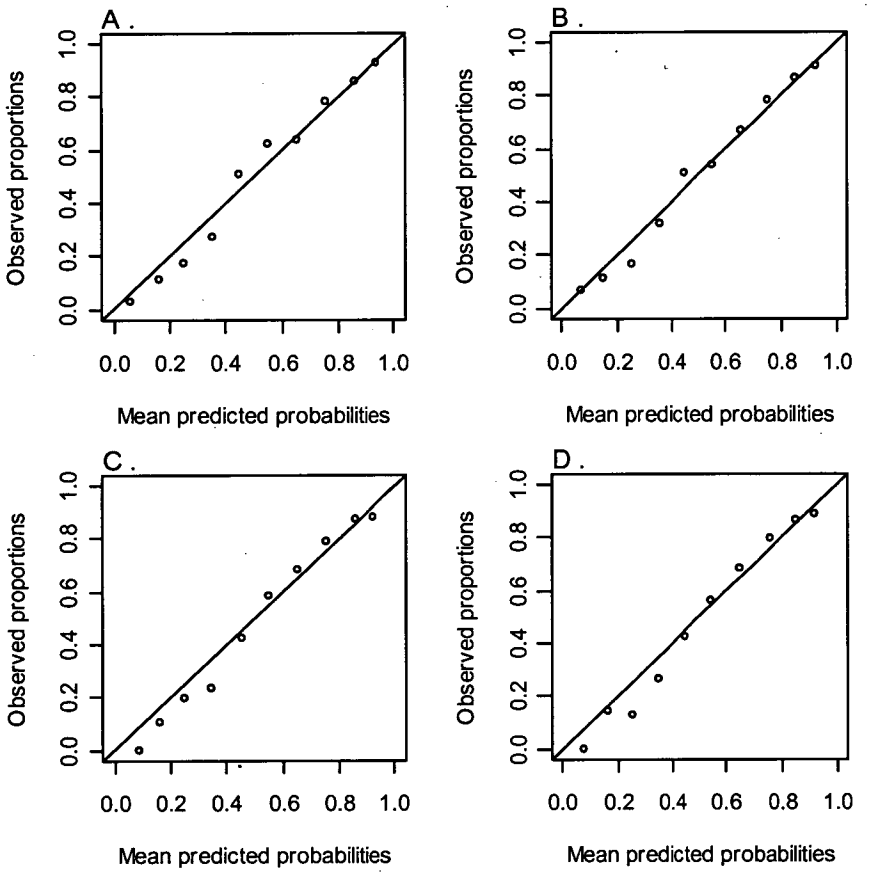

Fig. C2. Goodness of fit plots for (a) GLM with DOY (C = 0.78, D_{xy} = 0.55), (b) GLM without DOY (C = 0.76, D_{xy} = 0.51), (c) GLMM with DOY (C = 0.73, D_{xy} = 0.47), and (d) GLMM without DOY (C = 0.72, D_{xy} = 0.45). The range of possible expected probabilities is divided into ten equally sized bins, and the mean expected proportion of successes then plotted with the observed proportion of successes for the data points falling into each bin. Also given are the Somers' rank correlation (D_{xy}) and the corresponding index of concordance (C) calculated for each comparison of the predicted probabilities and observed binary outcomes.

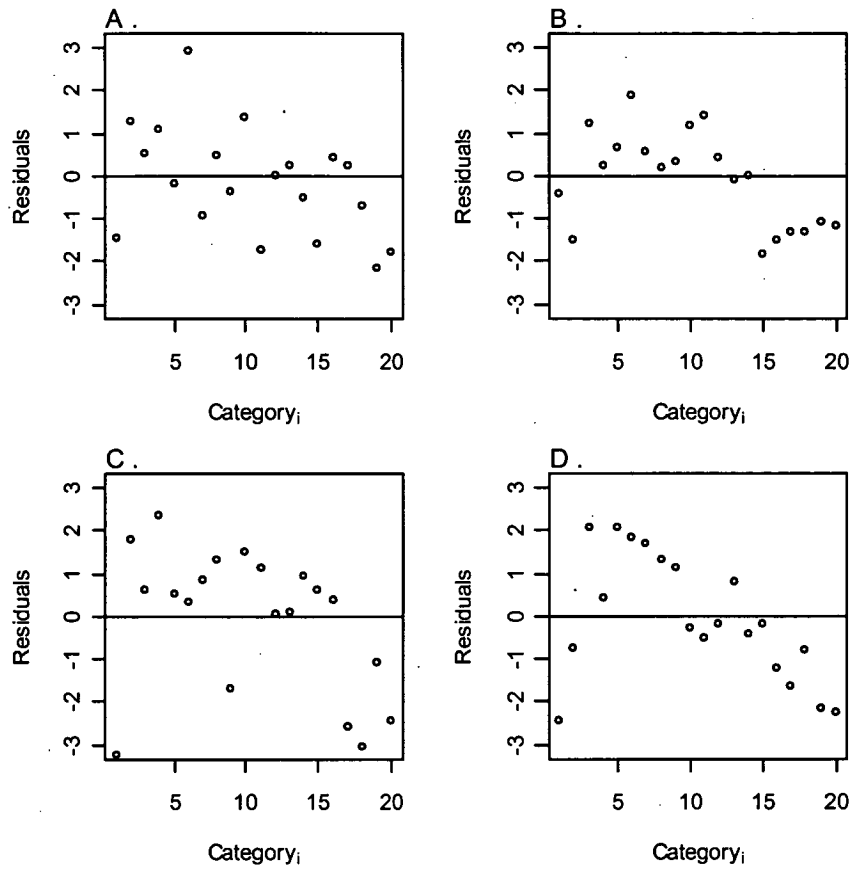

Fig. C3. Diagnostic plots showing approximate residuals A_i for (a) GLM with DOY, (b) GLM without DOY, (c) GLMM with DOY, and (d) GLMM without DOY. Residuals obtained by categorizing the predicted probabilities such that $n_i \bar{p}_i$ is approximately equal across all categories i (see methods for details).

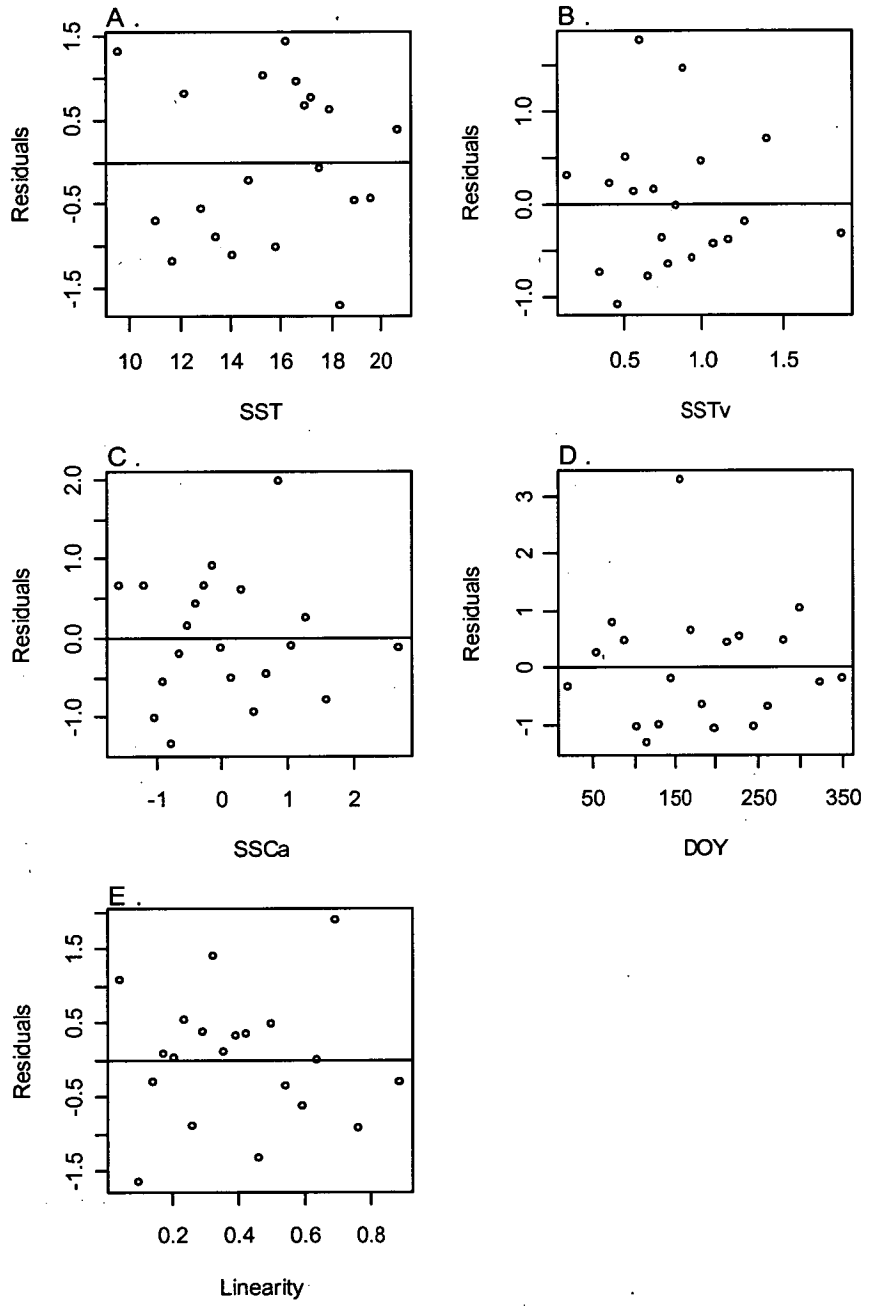

Fig. C4. GLM diagnostic plots categorising the predicted probabilities with respect to each continuous covariate (a) sea surface temperature (SST), (b) sea surface temperature variability (SSTv), (c) sea surface colour anomaly (SSCa), (d) day of year (DOY), and (e) linearity index (see methods for details). Results are shown for the GLM including the DOY term.

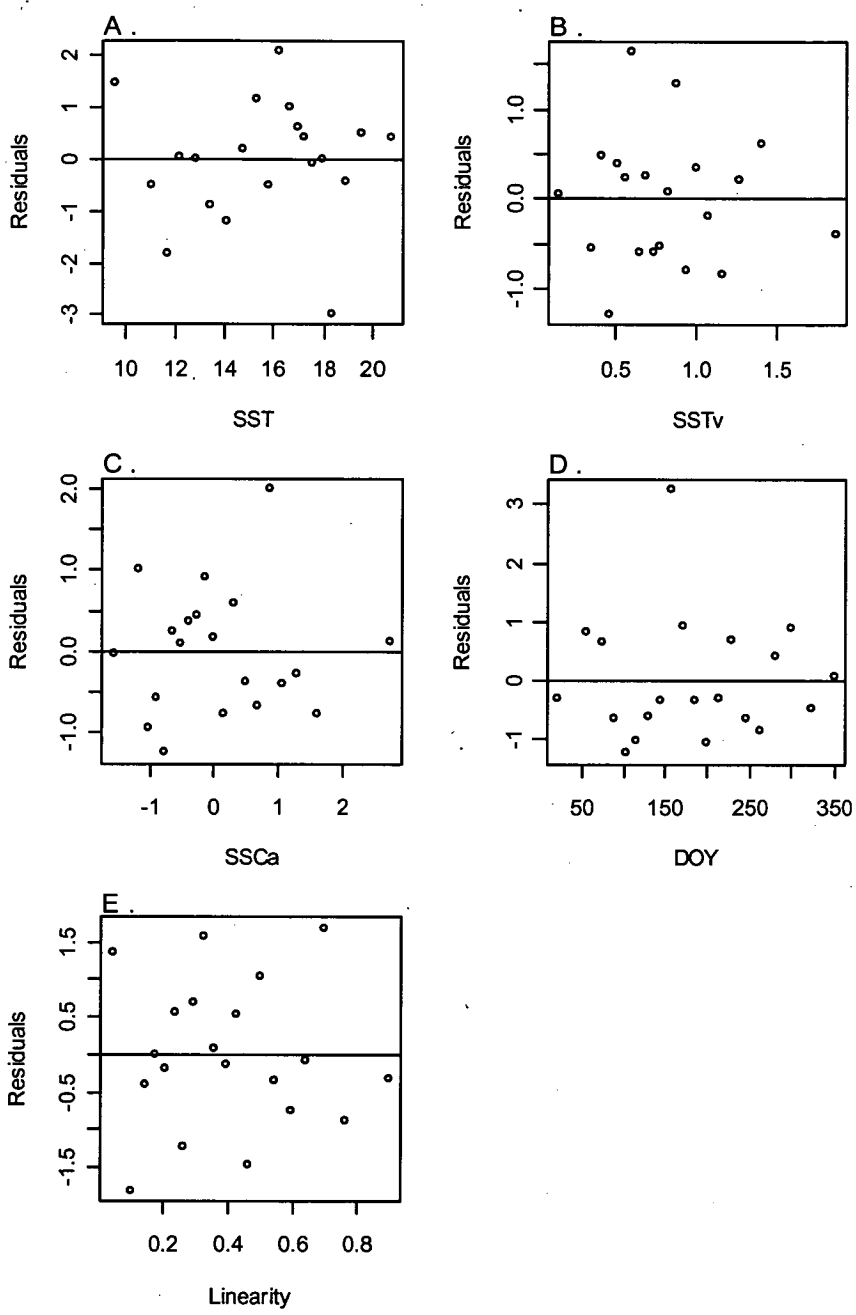

Fig. C5. GLMM diagnostic plots categorising the predicted probabilities with respect to each continuous covariate (a) SST, (b) SSTv, (c) SSCa, (d) DOY, and (e) Linearity index (see methods for details). Results are shown for the GLMM including the DOY term.

6. Synthesis and conclusions

This aim of this thesis was to investigate the long-distance migrations of a top order predator within an oceanographic context, and to determine environmental influences on movement and behaviour. This study has produced considerable new information on the annual migration of southern bluefin tuna through the integration, analysis and interpretation of telemetry-based and oceanographic data. A number of novel analytical approaches were developed to examine the timing and extent of the movements in the context of the seasonal temperate ocean (Chapter 2); the flexible vertical swimming behaviours adopted by the fish within different oceanic habitats (Chapter 3); and to quantify feeding success in relation to residency (Chapter 4) and to environmental characteristics (Chapter 5). These analyses provide a significant advance in our current knowledge on migration in marine animals, and an increased appreciation for the diversity and complexity of animal behaviour. In particular, the ability to detect feeding events from tag-based data provided sometimes unexpected insights into the motivations for movements and behaviours, challenging some existing ecological concepts.

Although in each chapter the results were interpreted within a broad ecological context, this discussion will provide a synthesis of the findings with respect to three major thematic areas that have repeatedly arisen throughout the work, and that lead to generalisations applicable across other species and studies: (1) linkages between biology and oceanography; (2) habitat use versus foraging, and (3) behavioural flexibility, individual variability and predictability. A final section will outline proposed future directions.

Chapter 6

LINKAGES BETWEEN BIOLOGY AND OCEANOGRAPHY

The integration of animal movement and behaviour with information on their physical environment remains a challenge for biologists studying migratory pelagic animals. The ongoing development of modern telemetry has been a revolution for the study of large, fast, actively diving and widely ranging species in the sense that the individual animals can tell researchers where they go, and when, and in various formats what they do there: we gain an organism-eye view. What remains to be interpreted is *why*, and placing the biology within the context of the physical environment, including often dynamic and complex oceanographic processes, is central to providing this understanding.

Tag-collected data is an important source of information, most commonly location, light level, temperature and depth information, but also more recently other environmental information such as salinity (Lydersen *et al.* 2002) or chlorophyll-*a* profiles (Teo *et al.* 2007a). The advantage of these data is that they are collected at a scale and resolution appropriate to the animal's behaviour. However further insights are gained when these tag data are integrated with other sources of environmental, data such as satellite derived products. This provides synoptic spatial and temporal coverage, and enables seasonal, interannual or other time-varying components of the oceanographic patterns to be determined and linked to the biology. Yet, relatively few studies have progressed to this point (but see Pinaud & Weimerskirch 2005; Polovina *et al.* 2006; Suryan *et al.* 2006; Teo, Boustany & Block 2007b).

This is partly due to the technical difficulties associated with accessing both data types, and processing the vast volumes of complex time-series resulting from both data sources. It is still common to report a few animal tracks overlaid on a few maps together with a detailed description of one or more 'representative' animals. Indeed, progressing to the next step of quantitatively assessing the relationships between physics and biology involves another level of statistical complexity. The spatial accuracy of the position information obtained from many electronic tracking methods, in particular light- or SST-based geolocation, has been an additional limitation (Teo *et al.* 2004; Domeier *et al.* 2005). The

resolution available for remotely-sensed data (*e.g.* 0.08° grid for SSC) is often well ahead of the spatial resolution of the tag location data. However, there are three particularly favourable aspects of the large SBT tagging data set: (1) the archival tags themselves provide detailed information on the local environment, particularly on the subsurface structure of the water column, (2) the scale of the positional inaccuracies is an order of magnitude less than the scale of the migratory movements, and (3) the impressive migratory movements take individuals through extensive variation in the physical properties of the habitats in which they forage. Therefore, the extensive environmental variation provided sufficient scope for developing some descriptive and predictive models for animal movement, behaviour and feeding.

In this thesis, a number of novel statistical approaches were developed to integrate the physics and the biology of the system. Traditional oceanographic techniques were applied to satellite fields to decompose the dominant seasonal patterns of variability, at an ocean-basin scale, and identify potential seasonal feeding habitats for SBT (Chapter 2). This approach qualitatively placed the timing and spatial extent of the migrations into the context of the regional oceanography, and identified three specific patterns of seasonally enhanced production (in terms of primary production and also water mass production) in areas used by migrating SBT. A second method used the tag-based data to directly characterise the oceanic habitats of SBT, in terms of vertical water column structure, and quantitatively modelled links between these habitats and vertical movements of the fish (Chapter 3). The influence of different oceanographic variables on the feeding success of SBT was then more directly examined through the final modelling study (Chapter 5).

The value of using multiple data types, from a range of tag-based and satellite-borne sensors, was evident as it enabled quite fine-resolution feeding and diving behaviours of individual animals during periods of active movement or residency to be integrated into the broader oceanographic context. Rather than identify a particular migratory destination, these studies all demonstrated SBT to exploit a mosaic of oceanic habitats between the subtropics and the subantarctic, some of which were more productive than others. Some habitats conformed to a

classic expectation of tunas associating with frontal features; in particular the Agulhas retroflection system can be considered a "biological hotspot", a region of intense biological production supporting critical ecosystem linkages. However, another frontal feature, the north Subtropical Front, was revealed as a relatively poor foraging zone (from the tag-based data on feeding events) and it remains unclear as to whether this situation is the norm or particular to the cohorts in this study. Perhaps most interesting, was the identification of a mode-water region as an important habitat. Juvenile SBT spent lengthy periods here, exhibited specific deep vertical movement patterns (Chapter 2 and 3), and showed high foraging success (Chapter 4 and 5). This association appears to be quite unique among migratory pelagic species, and the seasonal ecosystem structure and dynamics of this area deserves further investigation. The significance of deeper water mass features for foraging has recently been highlighted for other predators, for example southern elephant seals based on novel information about where body condition improves (Figure 4, Biuw *et al.* 2007). Notably, from the historical time-series showing the expansion and contraction of Japanese long-line fishing effort, this region appears to have been largely ignored (Tuck *et al.* 2003). This may be a consequence of the deep vertical behaviour of SBT in this region in fact making them unavailable to the longline gear.

These findings highlight the potential for a number of comparative analyses. Firstly, how do the movement and behaviour patterns of SBT in the Tasman Sea, an alternate migratory destination and an oceanic region of intense mesoscale variability and frontal activity, compare with those documented here? Secondly, is similar behavioural flexibility and wide usage of different oceanographic regimes exhibited by close-kin species, such as the Atlantic and Pacific bluefins? Both species are currently subjects of major tagging studies (Block *et al.* 2003; Block *et al.* 2005). Thirdly, what other top pelagic predators are sharing the South Indian Ocean with SBT during their seasonal appearance here, how do their patterns of resource use compare, and what are their interactions? Significant tagging (and other) data exist on a number of seabird (Tremblay & Cherel 2003; Pinaud & Weimerskirch 2005) and pinniped species (Guinet *et al.* 2001; Beauplet *et al.* 2004) to allow for a meta-analysis of top

predators within this region, and elucidate whether spatial, vertical, temporal or other (*e.g.* dietary) niche segregation or overlap exists.

HABITAT USE VERSUS FORAGING

The distinction between habitat use and foraging, often used interchangeably in the literature, was clearly demonstrated in this study. Habitat use is rarely given a clear definition and indeed may be used to describe almost any type of regional occupancy, usually over some period of time. For example, it may relate to the species' entire spatial and temporal distribution (Chapter 2), or occupancy of an area (Chapter 4), a habitat type (Chapter 3), or even more specifically of particular temperature or depth niches (Chapter 3). Habitat use may be in part determined by physiological constraints (*e.g.* oxygen limits, thermoregulation), learned behaviours (*e.g.* preferred migratory routes), or other influences such as social interactions. Habitat use is best examined within the context of the regional oceanography to evaluate the selection. Yet habitat use, utilisation or selection is very often used in tagging studies to infer foraging, whether from the movement data or diving data or a combination (Fauchald & Tveraa 2003; Jonsen, Myers & James 2007). Foraging though, is specifically dependent on the local prey field, and its availability, about which there are usually no direct data. So the same data, usually location, temperature, depth, are used to determine both habitat use and infer foraging behaviour.

The ability to identify the potential prey field, even indirectly, is often available from the vertical rather than the horizontal movements especially for species that exhibit specific foraging dives (Hindell, Slip & Burton 1991; Lea *et al.* 2002; Bost *et al.* 2007). Consequently, much effort has gone into developing objective classification systems of individual dives or dive bouts, for example for turtles, penguins and seals, to determine a measure of search effort (but not success). This approach is not applicable to species that exhibit free swimming behaviour, unrestricted by any air-breathing requirements, such as pelagic fishes. The most reliable way to allocate foraging function to behaviour is of course to obtain some direct information on feeding activity. While the visceral warming

patterns which occur in tunas are obviously unique to that taxa, many other novel approaches exist to identify feeding activity in a wide variety of marine animals. These include measuring stomach or oesophegal temperatures (Wilson *et al.* 1992; Gales & Renouf 1993; Austin *et al.* 2006a; Bost *et al.* 2007; Horsburgh *et al.* 2008), jaw angle (Liebsch *et al.* 2007), stomach pH (Papastamatiou & Lowe 2005), buoyancy (Biuw *et al.* 2003; Biuw *et al.* 2007), and vocal behaviour using echolocation (Watwood *et al.* 2006). Other methods such as accelerometers (Kato *et al.* 2006) may also be used to identify distinct predatory behaviours such as attack behaviour.

Having a direct measure of feeding success provided the most important insights and highlighted the complexity of SBT behaviour. Most prominent was the finding that time-spent within an area had no clear relationship with feeding success, across any scale examined, primarily due to the high degree of variation observed between individuals (Chapter 4). This indicates that areas of high-use for migratory species, as commonly determined from horizontal and/or vertical movement data in the absence of any independent information on feeding activity, should not be implicitly interpreted as successful feeding grounds. Whether this result stems from poor individual predator ability, variable prey availability, or alternate factors motivating residency, remains to be determined. Substantial archival tag data is now available for SBT from later releases (by CSIRO in 2002 and over 2004-2007) enabling further investigation as to whether (1) the high level of observed fish-to-fish variation is a consistent feature over all juvenile cohorts, (2) the identified regions of higher and lower feeding indices are pervasive features through time or variable between years, and (3) SBT show fidelity to particular regions. The association of top marine predators with specific oceanic features (for foraging, breeding, or as migratory corridors), and in particular the persistence or recurrence of those associations, is a major focus of current research efforts across taxa (Block *et al.* 2003). Developing this fundamental knowledge may provide insight into the evolution of species, and be of great importance in informing management and conservation measures for commercially valuable and depleted or protected species.

A second significant finding was that feeding success for juvenile SBT was generally high throughout most of their migratory range and in particular was elevated during directed periods of movement (Chapter 5). This does not conform to the widely held notion of predators making directed movements between patches of high feeding success. Instead, it may indicate SBT use multiple strategies including a combination of (i) continuous movement and extensive search behaviour efficient for finding isolated or dispersed prey, and (ii) extended periods of residency within particular areas in the open ocean. This migration model seems appropriate for opportunistic predatory species such as pelagic fishes which swim freely throughout the epi- to mesopelagic layers, and should not necessarily be constrained to suppress feeding during transit. It may be a more appropriate model for other migratory marine species that are generalist predators than is currently documented. Although at very broad geographic and seasonal scales animals may be have an awareness of resource distribution (Bradshaw *et al.* 2004b; Houghton *et al.* 2006), and at fine-scales foraging is likely to be dominated by proximal sensory clues (Sims & Quayle 1998), the mesoscale search strategies which animals use to locate prey remains a pivotal problem in ecology (Sims *et al.* 2006; Edwards *et al.* 2007; Sims *et al.* 2008).

Finally, the feeding success data gave the first insight into the nature of the benefit which SBT gain from their seasonal occupation of the Great Australia Bight. The GAB is clearly a "biological hotspot" for SBT, as they aggregate there each summer in high densities and show strong seasonal growth in length during this time (Eveson *et al.* 2004). Yet the feeding indices calculated for the region did not show a simple picture of a superior feeding habitat (Chapter 5). Rather, the model results showed that SBT may benefit from a more predictable, instead of a more abundant source of prey, and one which is available over a relatively long period of time. There may also be additional benefits associated with reduced costs, from hunting in schools and having lower daily travel distances. But overall, the less straightforward traits of the GAB "hotspot" open up broader possible interpretations of the role of animals within the biophysical systems in which they operate. For example, in seasonally fluctuating environments the evolution of annual migrations and fidelity to predictable foraging regions may

confer an ecological benefit to individuals over long time-scales even when energy gain is not high in all years (Schmidt 2001; Bradshaw *et al.* 2004b).

PREDICTABILITY, BEHAVIOURAL PLASTICITY AND INDIVIDUAL VARIABILITY

Tagging technologies provide large volumes of detailed and complex time-series data, but usually on relatively few individuals. Developing a synthesis of general patterns appropriate to populations and predictable across individuals is challenging from such detailed descriptions of movements and behaviour. A further challenge is determining the significance of observed variability among individuals, and appreciating real flexibility and complexity where it exists. Both are necessary in determining meaning from, and developing explanations for, the data.

In this study, mixed effect models were used to establish the statistical significance of observed patterns (Chapters 3, 4 and 5). These models take into account that there are multiple measurements on a single sampling unit (*i.e.* many observations per fish through time). The individual subject parameters are not modelled directly but as random effects. Depending on the circumstance, some models were also designed to include an explicit temporal correlation (Chapters 3 and 5). Mixed models provide many important advantages over standard approaches such as the repeated measures ANOVA. The assumptions about the data are much less restrictive, for example mixed models can allow for unbalanced data between individuals, missing data or repeated measurements taken at unequal time intervals. Most importantly, time effects can be flexibly modelled and realistic variance and correlation structures can be used, allowing the within-individual errors to be correlated and/or have unequal variances. Due somewhat to the complexity of the models their use has not yet become routine. However software for these types of models is likely to become much more widely used by the tagging community in the future.

Predictability

A range of predictable behavioural patterns were quantitatively determined across individuals in response to a variety of environmental factors. Vertical swimming behaviour, for example, varied between oceanic habitats and in relation to time of day and lunar phase (Chapter 3). The water depths and temperatures at which feed events were initiated showed variation between the seasons (Chapter 4). Predictable relationships were found across individuals between feeding success and ocean temperature, temperature variability and sea surface colour anomaly (Chapter 5). Consistent behavioural responses are therefore predictable among individuals at a variety of scales, including ocean basin and regional spatial scales, and seasonal, monthly or daily timescales. As discussed above, these analyses are amongst the first to quantitatively examine direct linkages between oceanography and the movement, behaviour and feeding of a migratory top order predator as elucidated by electronic tagging data. Yet a number of limitations were also apparent.

Foremost among these are the limited tools currently available for characterising the habitat of wide-ranging species. On one hand the synoptic coverage of surface variables available from remote-sensing provide an excellent insight into the ocean dynamics down to a resolution often well ahead of the spatial resolution of the tagging data used in this study. On the other hand, many steps of inference are required for the functional interpretation of observed behaviours with such tropho-dynamically remote parameters (*i.e* tuna don't eat surface phytoplankton) (see also Gremillet *et al.* 2008). In addition, limited information on subsurface habitat features of interest to pelagic predators is available, other than the information the tagged animals themselves provide. More localised studies, for example based around a single estuary or island, can directly sample habitat variables such as substrate type, percentage cover, community structure, and localised production and factors such as these may have a high predictive capability for the movements and behaviour of individuals through time. Studies of widely ranging pelagic predators continue to be challenging in this regard.

In particular, the feeding patterns of a top predator are likely to be driven by the abundance and type of prey field encountered, (*i.e.* patch-scale processes), and therefore should only be weakly correlated with the majority of imperfect environmental predictors available. It would of course be desirable that some field research be directed towards investigating ecosystem structure and dynamics in areas identified from tagging studies as of particular interest to important migratory species. However, the costs of such studies in many cases are prohibitive, and the data may ultimately represent a spatially and temporally restricted fraction of a species' prey distribution. An approach currently being investigated is developing model-based real-time estimates of prey fields (Lehodey *et al.* 1998; Lehodey *et al.* 2001; Lehodey *et al.* 2003). At present, while high-resolution data assimilating models are beginning to provide plausible ocean dynamics, coupling the appropriate biogeochemistry and nutrient-phytoplankton-zooplankton models to represent the trophic transfers remains an enormous challenge. In many cases animal-borne sensors for detection of feeding activity are providing more information on prey field distribution than is otherwise available, and are likely to be important for validating the emergent prey models.

Behavioural plasticity

A prominent feature to emerge from a number of the analyses was the level of behavioural plasticity displayed by juvenile SBT. Qualitatively this plasticity was apparent in the variety of oceanic regions and habitats which individual fish were capable of exploiting (Chapters 2 and 3). Quantitatively, behavioural plasticity was found in SBT vertical movements, for example with lunar and migration influences on swimming behaviour resulting in inconsistent diel patterns between different habitats. Lunar phase also had some influence on the time of day at which feeding occurred and foraging behaviour altered markedly between seasons (Chapter 4). In other words, particular diving and feeding behaviours were not necessarily fixed but adopted flexibly in response to a changing environment, and potentially a hierarchy of influencing factors. The result appears to be efficient

feeding success across a large migratory range and throughout highly variable coastal and oceanic environments (Chapter 5).

There is increasing evidence that behavioural plasticity is a common feature of a wide variety of marine predators. Most reports from tracking studies relate to plastic diving behaviours, which may change in association with the moon (Horning & Trillmich 1999), in different areas of a species range (Sims *et al.* 2005; Hays *et al.* 2006) or during different migratory phases (James *et al.* 2006). Variation in diving may coincide with variation in movement rates during different migratory phases (Jonsen *et al.* 2007). Such plastic behaviours are widely interpreted as a response to local prey distributions which are variable in space and time (Ryer & Olla 1995). An ability to behave flexibly enables a rapid and appropriate response to changing prey distribution and abundance, ensuring higher feeding rates and broader diets in the presence of environmental variability (Dill 1983), and hence improved survival. Research on captive animals (Warburton, Retif & Hume 1998; Odling-Smee & Braithwaite 2003; Rabin 2003) and in release programs (Olla, Davis & Ryer 1998; Braithwaite & Salvanes 2005) provides support for the links between environmental heterogeneity and flexible and adaptive behaviours. In highly mobile and opportunistic marine predators like tuna which inhabit a highly variable ocean environment, such plasticity is therefore perhaps an expected result of natural selection

Individual variation

In many cases, these analyses revealed relatively consistent responses by individual animals to environmental variables, however substantial individual variability was also a persistent feature of the data. Qualitatively, this was apparent in the specific timing of individual movements in and out of the summer grounds and the independent migration routes followed (Chapters 2 and 3). Quantitatively, significant fish-level variability appeared in all the analyses of diving and feeding behaviour (Chapters 3-5) and comparisons of model structures allowed these fish-level effects to be evaluated. However, the ultimate source of the individual differences remains unclear. One explanation may be that relatively few predictors have often been used, and these can be considered indirect or

imperfect in that they do not directly represent the prey field which predators are likely responding to (as discussed above). Better understanding of the proximate influences on behaviour may ultimately decrease the level of significance allocated to individual effects. However, individual variation is likely to be a real feature of behavioural and foraging ecology (Magurran 1993). Increasingly, theoretical frameworks are being developed around the ecological and evolutionary significance of the phenomenon of individual variability and more specifically, individual quality (Bolnick *et al.* 2003; Dall, Houston & McNamara 2004; Sih, Bell & Johnson 2004; Stamps 2007).

One proposed explanation for the maintenance of individual variation has emerged from research into behavioural syndromes *i.e.* suites of correlated behaviours along behavioural axes such as boldness-shyness, aggressiveness-timidity, or proactiveness-reactiveness (Sih *et al.* 2004). Maintenance of persistent behaviours may generate important ecological trade-offs, for example consistent boldness in foraging can effect increases in both growth rate and mortality rate (Stamps 2007). Consequently, the growth-mortality trade-off may result in consistently different individual behavioural traits generating a relatively flat fitness surface (Mangel & Stamps 2001). This might generalize broadly over other behavioural traits through various physiological processes, such as aggressiveness and metabolic rate (Ros, Becker & Oliveira 2006) or boldness and reproductive success (Godin & Dugatkin 1996). In an evolutionary context the functional connections between behaviour and physiology, and the trade-offs engendered, may therefore provide some explanation for the maintenance of individual differences in behaviour in animals. Within pelagic animals, individual differences may represent yet another characteristic contributing to survival and resilience in a complex and variable environment.

Applications for electronic tagging data

Electronic tracking can provide valuable qualitative information on movement patterns and the potential vulnerability of marine predators to human activities. Examples of these include documenting the presence of threatened species within areas of fishing activity (Nel *et al.* 2002; James, Ottensmeyer & Myers 2005; Southall *et al.* 2006) or survey efforts (James, Myers & Ottensmeyer 2005); showing that distributions of fished populations currently managed as separate stocks are in fact overlapping (Block *et al.* 2005); or highlighting potential competition between natural and human consumption of a resource (Field *et al.* 2004). Two major quantitative applications that involve the use of electronic tag data are (i) habitat-based standardisation of catch per unit effort data used in fisheries stock assessments; and (ii) prediction of habitat preferences and potential impacts of climate change. The findings of this thesis highlight the potential dangers of an overly simplistic approach to both of these issues. Both need to be pursued with due consideration to the flexibility and complexity of individual behaviours, and the issues involved in scaling up from the individual to the population, and indeed ecosystem, level of the ecological processes being modelled.

A substantial amount of research has been devoted to determining the habitat preferences and limits, *i.e.* habitat envelopes, of pelagic species from electronic tag data. Such models of habitat preference most commonly involve time-at-temperature and/or time-at-depth. (Bigelow & Maunder 2007) give a good initial summary of the dangers inherent in the deterministic application of such tagging data to standardizing CPUE. These can be expanded upon and generalised to include other attempts at predicting a species' habitat preferences, and most particularly at extensions of these predictions into climate-change simulations.

Most prominently, habitat preferences are usually derived from a limited number of individuals, so whether a population or species is adequately represented is doubtful. In the few cases where large numbers of individuals have been tagged, most studies suffer from a limited experimental design prohibited by time, cost and sometimes jurisdictional issues from being able to choose release

sites across a species range. Where such large-scale data are available, significant variability in behaviour between sub-populations has been observed (Righton, Metcalfe & Connolly 2001; Neat & Righton 2007). Secondly, the habitat preference data is usually available at restricted spatial and temporal scales. This study, and others showing the behavioural plasticity of marine predators in response to varying ocean dynamics, indicates that the extrapolation of habitat preferences between geographic regions is likely to be inappropriate. Plausible results for habitat prediction have been obtained within a restricted geographic area over specific short time-frames (Hobday & Hartmann 2006). Yet to evaluate the effects of inter-annual and longer scale climatic variability on observed habitat preferences requires time-series data which are rarely available.

Thirdly, there is likely to be a spatial/temporal mismatch between the environmental data available for predicting habitat (*e.g.* model-based time-averaged spatially stratified data), and the near-real time habitat preference data of a (perhaps non-average) individual. Fourthly, habitat preferences or envelopes may not adequately represent real biological processes if they fail to consider the motivations for habitat use in the first instance. For example, our analyses suggest juvenile SBT may have alternative motivation for occupancy of areas other than feeding (chapters 4 and 5). This could influence vulnerability to capture, as well as imply different consequences of climatic change between habitats. Further, marine predators can show changes in behaviour in response to diurnal, lunar, seasonal, or ontogenic cycles, as well as reproductive cycles. These complex temporal components are difficult to account for using simplistic habitat envelopes. Finally, the high degree of individual variability highlighted in this and other studies is itself a challenge largely ignored, and to our knowledge never addressed in a quantitative manner (beyond say the statement of a simple variance estimate for a parameter of interest) in the use of electronic tagging data to predict habitat preferences.

Electronic tagging provides invaluable information on fish behaviour which is otherwise difficult and costly to study. Appropriate statistical analyses of the data can help elucidate what environmental variables are important in influencing behaviour. From this we can then develop ecological inferences about

the oceanic and biological processes underlying the observed behaviour. These findings can be used to inform the analysis and interpretation of other long-term data sets, such as demographic indices or survey/catch data (*e.g.* Rolland, Barbraud & Weimerskirch 2008). Such an approach can provide valuable insights into the likely influences of climate variability and change on animal distributions. In particular, developing a real understanding of the biological function and importance of different oceanic systems to marine predators will be fundamental to predicting the effects of change. The result is likely to be far more complex, and perhaps more subtle, for example than predicting a simple poleward shift in cold-adapted species (Parmesan & Yohe 2003; Poloczanska *et al.* 2007). Rather, we may need to consider the possibility of the slow-down or shut down of an entire oceanic system and the likely consequences for the entire reliant ecosystem.

FUTURE DIRECTIONS

This study has produced new insights into the annual migrations of southern bluefin tuna through the integration of biotelemetry and oceanographic data. Future efforts towards advancing our knowledge of movement in marine animals will benefit from continuing to develop these types of linkages across diverse disciplines. Animal migration and the emerging themes of behavioural plasticity, individual variability and predictability involve elements of behavioural and foraging ecology, morphology and physiology, genetics and evolution, ecosystem processes, ocean dynamics and more. Three key areas for immediate future directions are (i) improved quantitative integration of biological and oceanographic data, including the development of appropriate tools for habitat characterisation and the major challenge of prey field estimation; (ii) a movement towards larger scale studies in terms of both numbers of individuals to get at population level patterns, and number of species to get a synoptic picture of oceanic ecosystems; (iii) development of integrated energetics models to evaluate the physiological costs and benefits of migration in marine predators.

(i) *Oceanographic linkages*. Providing an oceanographic context for the movement and behaviour of marine predators is a primary objective of many contemporary studies, and much has been written about this already. Currently tag developments are exploring more sophisticated sensors to measure water salinity (Lydersen *et al.* 2002) and chlorophyll profiles (Teo *et al.* 2007a), which provide physical measurements at the scale most appropriate to the animal. The use of external environmental information is limited by the relatively coarse spatial resolution of the geolocation position estimates (Teo *et al.* 2004; Domeier *et al.* 2005), but good results can be obtained from large-scale analyses. As geolocation methods improve (Royer, Fromentin & Gaspar 2005; Nielsen & Sibert 2007; Patterson *et al.* 2008) so too should our ability to analyse relationships with features such as mesoscale eddies and fronts (Rodhouse *et al.* 1996; Nel *et al.* 2001; Cotte *et al.* 2007).

Complementary to this is the development of regional to ocean basin scale modelling systems for linking ocean dynamics, biogeochemistry, mid-trophic production and marine predator ecology currently being pursued at a number of institutes (*e.g.* University of Hawaii, IRD, SPC, and CSIRO). This avenue could provide more information on the prey fields underpinning spatial movements such as foraging and migration. Yet the investigation of fine-scale processes (Sims & Quayle 1998; Fritz, Said & Weimerskirch 2003) is always likely to remain beyond the scope of daily geolocation resolution, making it difficult to examine the patch-scale events that feeding actually constitutes. These fine-scale questions may be more approachable using the high-resolution information tags provide on vertical movements (*e.g.* Sims *et al.* 2008). Good opportunities certainly remain for further analyses linking movement, vertical behaviour and feeding events (*e.g.* Austin *et al.* 2006b) potentially at nested scales.

(ii) *Synoptic studies*. Detailed information obtained from a handful of animals, whilst providing an intriguing level of detail on individual behaviour makes it difficult to determine the generality of trends and to scale up to population level interpretations. Two simultaneous developments are allowing progress on this issue (1) increased availability, variety and affordability of tagging technologies, and (2) development of broader international collaborative

programs. The result is an emergence of larger scale multi-species studies enabling a synoptic picture of oceanic ecosystems to be developed. The current main examples fall under the Census of Marine Life (www.coml.org), *e.g.* the projects EUTOPIA (European Tagging of Predators in the Atlantic; Sims *et al.* 2008), TOPP (Tagging of Pacific Predators; Block *et al.* 2003), and POST (Pacific Ocean Shelf Tracking; Welch, Boehlert & Ward 2002). However, to get at population level processes there is a need to undertake more targeted research. Most importantly, rather than simply tagging more individuals in conveniently accessible or affordable locations, some preliminary assessment is necessary to determine both the minimum number of deployments required (Hindell *et al.* 2003) and what spatial design will give the most information and a coherent coverage of the species known distribution.

(iii) *Energetics models*. The remarkable biology of bluefin tunas and the long-term feeding data available from the archival tags provides a unique opportunity for elucidating free-ranging energetics. In the present study, the analyses were largely limited to examining the presence or absence of feeding. The obvious next step is to properly unravel the calorific signature from the internal temperature trace using a mathematical thermodynamics model for metabolic heat generation. This approach can potentially quantify the energetic costs and benefits underpinning the long distance migrations. In particular, the relative value of prey taken during transit or in particular seasons or areas, would enable a better evaluation of the proposed continuous-foraging migration model. While relatively little physiological study has been undertaken on SBT, there is considerable information available for closely related tunas (Brill 1987; Brill & Bushnell 1991; Korsmeyer & Dewar 2001; Blank *et al.* 2007) and some promising advances on SBT metabolism have come out of recent caged mesocosm experiments (Fitzgibbon *et al.* 2006; Fitzgibbon *et al.* 2007).

A concurrent approach would be the development of a method to measure body condition, for example lipid content of tagged individuals (Willis & Hobday 2008). Buoyancy measures obtained for southern elephant seals have been used to provide a good indication of where and when individual animals are depositing fat and improving their condition (Biuw *et al.* 2003; Biuw *et al.* 2007). A measure of

fish condition in combination with the existing feeding information available for SBT could provide further important insight into the relative value of different foraging areas as well as on growth and energetics throughout and between migrating seasons.

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Appendix A. Annual cyclic migrations of 10,000 miles: juvenile southern bluefin tuna provide new perspectives on the limits of migratory behaviour in tunas

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Appendix A

SUMMARY

Populations of tunas and other oceanic apex predators are depleted globally, yet the spatial dynamics, population structure and habitat use of most species remain poorly understood. We report results from an electronic tagging experiment on juvenile Southern Bluefin Tuna (SBT), one of the world's most depleted oceanic fishes, in an effort to determine migratory patterns and the physical and biological motivations for migration. We show annual, cyclic, trans- and inter-oceanic migrations, spanning tens of thousands of kilometres, in the southern Indian, Pacific and Southern Oceans. Juvenile (3-5 year old) SBT exploit sub-tropical-to-sub-Antarctic waters ranging between 3.5-25.7°, and in the Indian Ocean "hotspots", often associated with bathymetric features, are systematically targeted by individuals. Internal body temperature records indicate consistent feeding success throughout all habitats, however, feeding depths vary markedly during a migration circuit, from near surface to 300m. Our results indicate SBT to be a highly-adapted, flexible predator, occupying a wide ecological niche. Importantly, fish spend a significant portion of the year outside the fishing grounds where they are targeted by high seas longline fleets, and the annual migration cycles and habitat use patterns revealed by the electronic tags present a significant challenge to the conventional standardization and uses of catch rates as measure of abundance. Caution is warranted in drawing conclusions about population changes simply based on trends in nominal catch rates.

Appendix A

BACKGROUND

Southern bluefin tuna (Thunnus maccoyii, hereafter SBT) are large, endothermic, long-lived and highly mobile oceanic fishes (Caton 1991; Kalish *et al.* 1996). Although juveniles and adults have almost circum-global distributions across the temperate latitudes (30-50S) of the southern Atlantic, Indian and Pacific Oceans, the species has a single known spawning ground south of Indonesia (Farley & Davis 1998) and is assumed to constitute a single stock on the basis of mitochondrial genetic analyses (Grewe *et al.* 1997). High levels of exploitation since the 1950's have reduced the spawning stock biomass to between 3-14% of pre-exploitation levels (Basson *et al.* 2004) and the species is listed as critically endangered under the IUCN Red list, on the basis of both abundance and exploitation indices (IUCN 2004). Despite this tenuous status, commercial fisheries worth about $US 0.75 billion p.a. continue to target SBT under the management of the international Commission for the Conservation of SBT. The Commission set a global catch limit of 14,930t for 2004 while the total catch (including Illegal, Unregulated and Unreported landings) was estimated to be in excess of 18,500t.

The study of animal movements and habitat utilization has been a central focus in ecological research providing one critical component for understanding population regulation, species interaction and community/ecosystem structure. Coinciding with the severe depletion of the SBT resource, the spatial extent of SBT longline and surface fisheries has contracted significantly over the last three decades, a change hypothesized to be a strong indicator of significant changes in population range and structure. However, as with many top pelagic predatory fishes, our understanding of the population and spatial dynamics of SBT comes almost exclusively from fishery catch and effort data and returns from conventional tag release-recapture experiments. Neither of these types of data provides information outside the areas where fishing occurs. The patterns of tag returns essentially mirror the distribution of fishing effort, with the added complexity of differential reporting rates across the range of fleets that exploit the population (Polacheck *et al.* 1996). Not only do we get a limited picture of movements – we also get a biased one.

Appendix A

The recent development of archival and satellite tags (Gunn *et al.* 1994; Metcalfe & Arnold 1997) has revolutionized the study of the spatial dynamics of large oceanic predator populations (Block *et al.* 2001; Bonfil *et al.* 2005). Since 1993 we have used this new technology to document movement patterns of immature (2-4 year old) SBT (Gunn & Block 2001) and in the process challenge some long-entrenched fishery-dependent paradigms. Here we show the truly phenomenal annual cyclic migrations over ocean-basin scales undertaken by juvenile SBT. The movement, behavioural and physiological data reveal SBT as a highly evolved, opportunistic predator targeting specific widely-dispersed oceanic "hotspots"(Worm, Lotze & Myers 2003) and capitalizing on a heterogeneous and seasonal environment. Moreover, the cyclic migration patterns and flexible ecology of the species provide significant challenges to existing stock assessment and management.

TAG DEPLOYMENTS

Between 1993 and 2000 in the Great Australian Bight (GAB) 525 juvenile SBT were implanted with archival tags which recorded depth, ambient and internal temperature and ambient light (Gunn *et al.* 1994; Gunn & Block 2001). To date, 124 (24%) tagged tuna have been reported recaptured, as far as 5521 nm from the release location, with a maximum time at liberty of 3561 days. Long-term data sets were obtained from 56 of the tags returned. Daily position and horizontal movement patterns were estimated from tag and environmental data (Hill 1994; Domeier *et al.* 2005), with individual tracks of between 57 and 493 days obtained. Furthermore, increases in the visceral temperatures of SBT associated with digestion (Stevens & McLeese 1984) were recorded by the internal temperature sensor on tags, and provided a record of feeding activity and a means of estimating daily ration (Gunn *et al.* 2001) for each day at liberty.

Appendix A

ANNUAL CYCLIC OCEAN-BASIN MIGRATIONS

The electronic tagging data reveal regular, ocean-basin scale, cyclic migrations undertaken by SBT as juveniles (Fig. A1). Following their austral summer residency in the shelf waters of the GAB, SBT show rapid, directed movements westward into the southern Indian Ocean (n = 36, 64%), eastward into the Tasman sea (n = 11, 20%), or more regional movements into the waters to the south of the GAB (115-145E) around Australia (n = 9, 16%). One individual moved substantively in both directions (108E-156E) within a single cycle at sea. The reason why individuals elect to move eastwards or westwards is unknown but it does not appear to be linked to size or age. The east-west displacements range between 1009 and 5003 nm and the summed daily east-west movements average 12429 nm (SD ± 4710 nm, range: 4159–25809 nm). Incorporating latitudinal movement this figure rises to 17923 nm (SD ± 6294 nm, range: 6708–34277 nm). In each year the migration phase generally began following the autumnal equinox, suggestive of a population stimulus such as change in day length. The return phase of the migration generally followed either the spring equinox or the summer solstice, resulting in early- and mid-summer returns to the GAB respectively. With a single exception all fish with sufficiently long tracks showed rapid movement back into the GAB over a period of 1–2 months, and residency throughout the following summer. Notably, of the 75% of fish ultimately recaptured within the GAB, 21% of these were actually recaptured during their second or subsequent year after release. This strongly suggests that individuals undertake these annual migrations for several years. Length-frequency data from the commercial fishery indicates that juvenile are less commonly found in the GAB from age five onwards (Eveson, Laslett & Polacheck 2003).

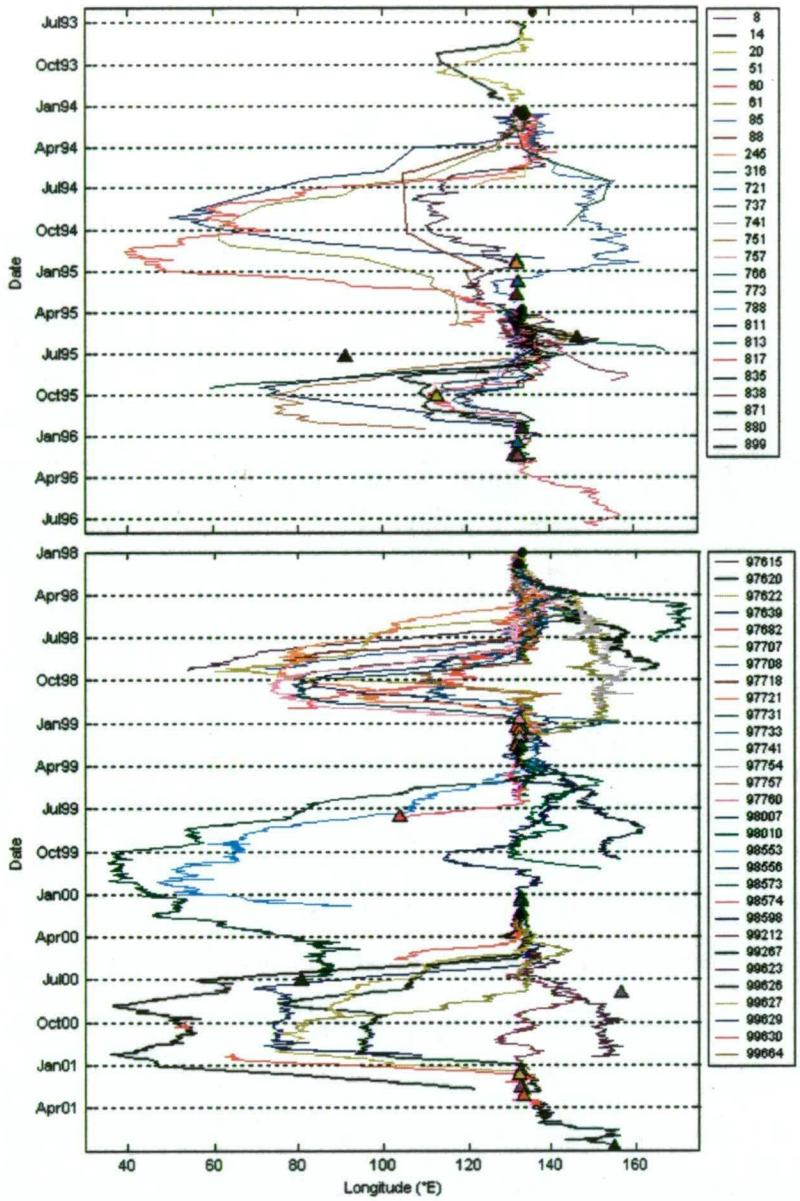


Fig. A1. Longitude tracks show large-scale cyclic annual migrations of juvenile southern bluefin tuna implanted with archival tags in the Great Australian Bight during 1993-2000. a, Fish tagged between June 1993 and March 1995 with Zelcon Technic P/L SBT100 (n = 8), SBT150 (n = 3), or SBT200 (n = 15) tags. b, Fish tagged between January 1998 and March 2000 with Wildlife Computers Mk7 tags (n = 30). All fish leave the summer feeding grounds during late autumn or early winter and migrate into the Indian Ocean or the Tasman Sea. Return migrations begin in the spring quarter. Longitudes are determined using light-based geolocation. Gaps in the track from SBT99630 (red, lower panel) are due to two periods when the light transmission failed (between 19 May – 28 September 2000 and 14 October – 5 December 2000). Circles represent release longitude and triangles represent recapture longitude. 1993: n = 2, mean size at release 88.5 ± 0.71 cm LCF. 1994: n = 8, 98 ± 1.91 cm LCF. 1995: n = 16, 91.06 ± 8.07 cm LCF. 1998: n = 16, 97.38 ± 2.96 cm LCF. 1999: n = 6, 102.83 ± 6.43 cm LCF. 2000: n = 8, 101.88 ± 2.95cm LCF.

After their extensive winter migrations 90% of the GAB recapture locations showed a net movement of less than 100 nm (and as low as 3.9 nm). This highlights an exceptional navigational ability of SBT. Although the exact mechanism remains unknown, it appears that within the GAB SBT may be homing to small-scale bathymetric features such as rocky reefs (Davis & Stanley 2002). It is notable in this regard that that there are no instances where the electronic track indicate that tagged fish migrated together (Figs A1 and A2) although more than a single tag was frequently released on the same day at a single location. Nevertheless, it is quite common for school members to be recaptured back in the GAB within days or weeks of each other. Thus, the archival tag data reveals very low school fidelity. If only the release and recapture location data were available, as would be the case in conventional tag-recapture experiments, we would most likely have reached the opposite conclusion. The lack of school fidelity would suggest that the ability to undertake these long distance migrations is not a learnt response from following older individuals.

Tag electronic failures mean we have very few archival data sets covering two successive winters. However, for two fish our data indicate a switch between westerly and easterly winter migrations in successive years - rare documentation of inter-oceanic migration. At least one individual is known from the electronic tag data recorded to have switched which ocean it occupied from one winter to the next. This individual spent its first year at sea in the southern Indian Ocean (as far as 75E) and following its second summer in the GAB moved into the Tasman Sea where it was recaptured (154.67E, 39.8S). For another individual, the electronic data show that it spent its first winter after release in the southern Indian Ocean (as far as 78E) and although the electronics failed it was recaptured in the Tasman Sea during the third winter (156.47E, 39.13S). No cases exist of the reverse inter-ocean movement from the Tasman Sea to the Indian Ocean.

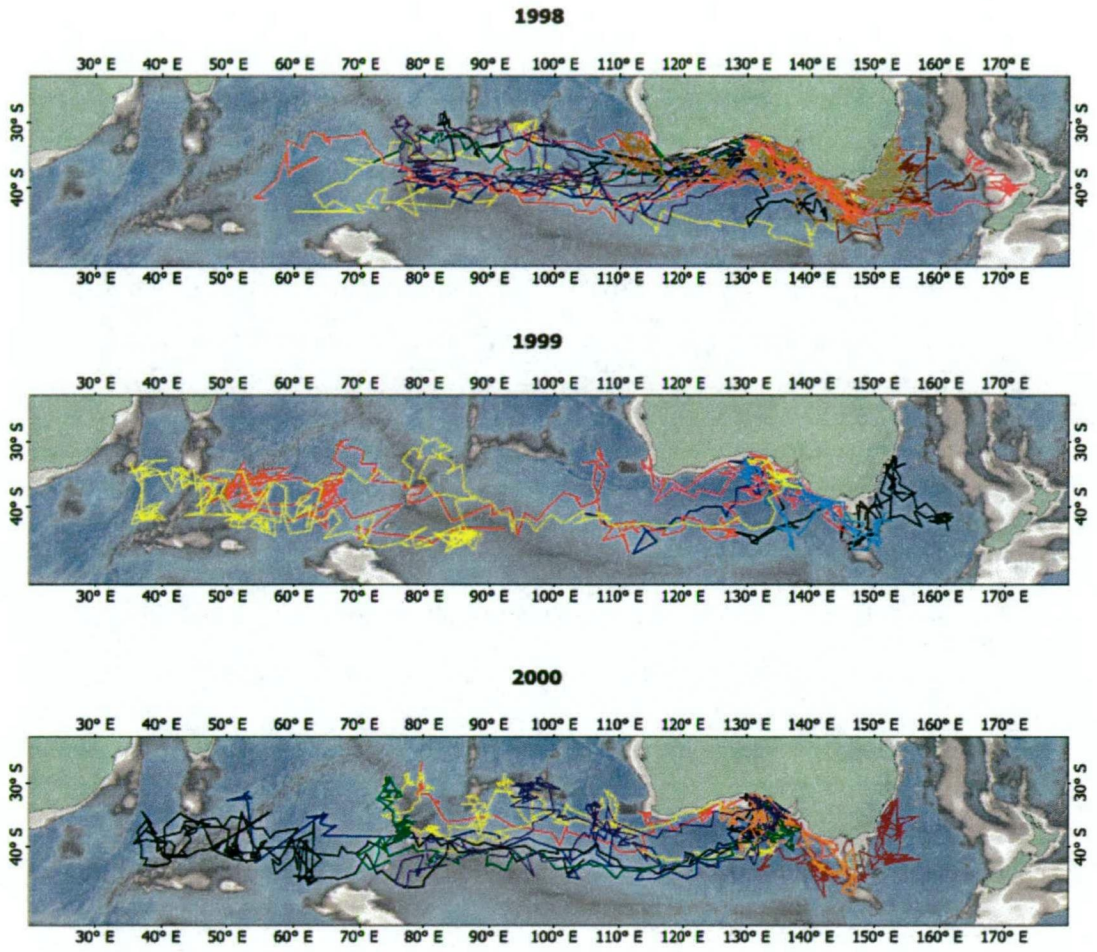


Fig. A2. Annual movements by juvenile southern bluefin tuna demonstrate systematic targeting by many individuals of "hotspot" areas in the southern Indian Ocean, particularly regions around prominent features such as plateaus and seamounts. a, Fish tagged in January 1998 (n = 16, N = 4111 positions). b, Fish tagged in March 1999 (n = 6, N = 1603 positions). c, Fish tagged in February 2000 (n = 8, N = 2238 positions). Positions are estimated using light-based geolocation and sea surface temperature. Background shows ocean bathymetry.

The term "migration" is often confounded with simple movements in the description of behaviour. We consider migration to apply to directed movements (often of long-distances) that occur across individuals and with regularity in the life cycle of a species. Migrations evolve to take advantage of the spatial and/or temporal differences in the distribution of resources (*e.g.* seasonal peaks in prey abundance; appropriate spawning habitats). The large scale cyclic migrations revealed here for juvenile SBT have not been found among other species normally considered to be "highly migratory". Previously documented migrations among large pelagic fishes are associated with spawning. While large scale movements outside of spawning have been recorded for individuals these appear to episodic, and cyclic ocean-basin migrations were previously unknown (Itoh *et al.* 2003a; Wilson *et al.* 2005). As such, SBT represent one of the world's most highly migratory species. The extent to which this is a unique feature of SBT, or a limitation of existing data in other species, is uncertain. Notably, previous conventional tagging of juvenile SBT, involving hundred of thousands of releases, provided no indication that such migrations were occurring.

PELAGIC HOTSPOTS

The position estimates indicate that certain oceanic areas are systematically targeted by many migrating individuals supporting the concept of pelagic 'hotspots'(Worm *et al.* 2003). In the southern Indian Ocean these include the regions around prominent features such as plateaus and seamounts. Around the Southwest Indian Ridge (35-55E, 35-45S), Amsterdam Island (70-90E, 35-40S), and Naturaliste Plateau (108-113E, 33-38S) are three such areas of substantial aggregation (Fig. A2). Strong bathymetric features influence current flow and may be associated with intensified frontal zones, mesoscale eddy activity and/or enhanced primary productivity (Read *et al.* 2000). Foraging studies of island-based top predators (e.g seals (Beauplet *et al.* 2004) and albatrosses (Weimerskirch & Wilson 2000) breeding on the central and western South Indian Ocean islands) reveal spatial overlap with the some of the pelagic "hotspots" documented here. However, increased position densities are also observed in the central Indian Ocean along the southern boundary of the sub-tropical gyre (70–

100E, 30–35S) - an area not previously identified as a likely "hotspot" for pelagic predators. Eastward migrating SBT, in contrast with their westward counterparts, tend to display less rapid or directed movements. These fish generally travel south through the feeding grounds around Tasmania (Young *et al.* 1997) and then disperse widely throughout the eastern Tasman Sea (150-165E, 35-45S), most likely targeting transient eddies and filaments of the dynamic East Australian Current.

FEEDING, MIGRATION AND THE ECOLOGICAL NICHE OF SBT

Unique data on the frequency and magnitude of feeding events throughout an annual migration circuit have been obtained from the internal temperature sensor on archival tags. The data show SBT commenced feeding on average 16 days (SD ± 9 days, range: 4 - 38 days) following surgery, and feeding events were subsequently recorded on 84.5 ± 6.6% of days. The predicted mean daily intake was 0.84 kg (SD ± 0.53 kg, range: 0.02-5.94 kg), *i.e.* 4.18% (SD ± 2.69) of body mass, and this did not vary substantially between regions or decrease during migrations (Table A1, Fig. A3). Tuna are estimated to be capable of eating up to 30% body mass per day (Kitchell *et al.* 1978), however estimates of wild consumption from other *Thunnus spp.* are between 4-7% (Olson & Boggs 1986). Although some of our estimated intakes were as high as 29.5% of body mass, 97.2% were less than 10% of body mass. Therefore our calculated ration for juvenile SBT lies within the lower range of published estimates for endothermic scombrids. While the metabolic and aerobic capabilities of SBT have not as yet been directly measured, sustained travelling speeds of 2.6 L s^{-1} have been observed by ultrasonic tracking (Davis & Stanley 2002) and, taking into account the geolocation precision, the movement rates calculated here for migrating SBT are also within the range of optimal swimming speeds previously calculated for migratory tunas (1.5–3 L s^{-1}) (Korsmeyer & Dewar 2001).

Metabolic digestion costs (Specific Dynamic Action – SDA) can represent a large proportion of aerobic metabolism. Typically, SDA is thought to account for 15% of ingested energy in fishes and maximum oxygen consumption

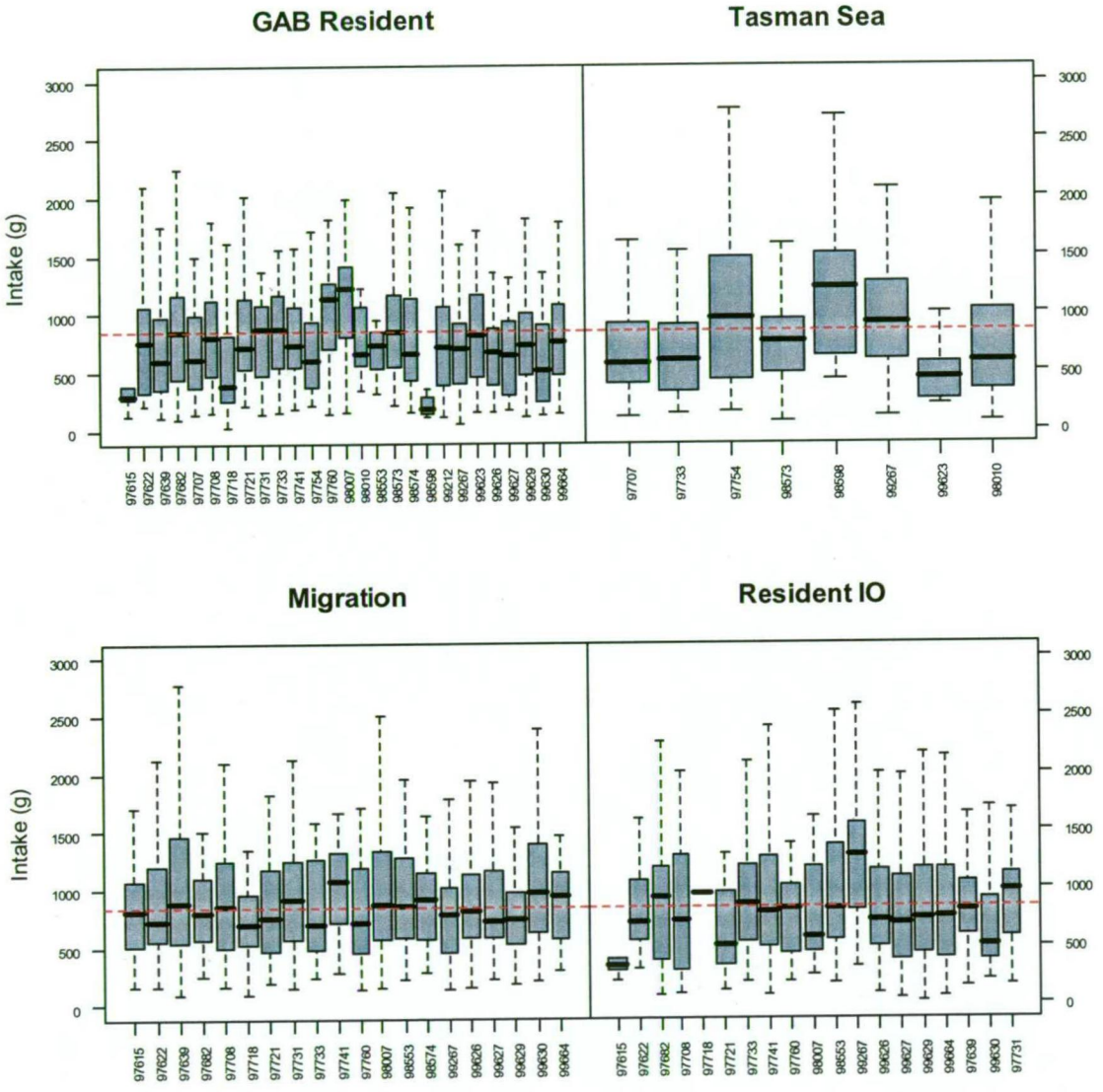
following feeding can be 1.5-2.5 × Standard Metabolic Rate (SMR) (Korsmeyer & Dewar 2001). This means that activity costs and repayment of oxidative debt and SDA are likely to exceed maximum aerobic capacity. In tuna, these problems are likely to be made particularly acute by high SMR and the required constant swimming for ram ventilation. However, our data gives no evidence for a trade-off between digestion and activity as migrating fish exhibit no signs of decreases in ingestion amounts. Our data are consistent with the theory that tunas have evolved physiological mechanisms to increase aerobic scope to enable constant swimming and high rates of consumption and digestion (Korsmeyer & Dewar 2001). It is likely that through large aerobic scope and the evolution of endothermy, which allows for increased aerobic capacity of oxidative muscle tissues (red muscle), SBT are able to feed, grow and migrate simultaneously.

Table A1. Average daily feeding frequency, intake and movement rates during four migration phases for wild juvenile SBT released 1998-2000. All results are reported as means ± s.d., with value range shown in brackets.

	Feeding			Movements	
	Frequency (d^{-1})	**Mean Intake (kg)**	**% Body Weight****	**$nm.d^{-1}$**	**$L.s^{-1}$***
GAB	0.82 ± 0.67	0.792 ± 0.48	3.94 ± 2.43%	35.36 ± 11.96	0.76 ± 0.26
		(0.02-3.976)	(0.10 - 19.79%)	(15.64–62.96)	(0.34–1.35)
Indian Ocean	0.78 ± 0.64	0.88 ± 0.57	4.38 ± 2.84%	61.82. ± 18.71	1.33 ± 0.40
		(0.027-5.94)	(0.14 - 29.56%)	(39.18–99.69)	(0.84–2.14)
Migration	0.85 ± 0.62	0.92 ± 0.561	4.57 ± 2.79%	48.56 ± 20.47	1.04 ± 0.44
		(0.089-4.94)	(0.44-24.5%)	(16.22–111.18)	(0.35–2.39)
Tasman Sea	0.97 ± 0.63	0.830 ± 0.517	4.13 ± 3.29%	82.22 ± 29.00	1.77 ± 0.62
		(0.068-3.95)	(0.34-19.65%)	(43.22–185.12)	(0.93–3.98)

*Movement rates as length per second ($L.s^{-1}$) are derived using the global mean length at release (99.67 ± 4.48 cm LCF, range = 90–111 cm).
** Based on a global mean body weight of 20.1kg, calculated from the global mean length at release and a length to weight conversion.

Fig. A3a-d


GAB Resident
Tasman Sea
Migration
Resident IO
Intake (g)
0
500
1000
1500
2000
2500
3000
97615
97622
97639
97682
97707
97708
97718
97721
97731
97733
97741
97754
97760
98007
98010
98553
98573
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97682
97708
97718
97721
97731
97733
97741
97760
98007
98553
98574
99267
99626
99627
99629
99630
99664
97615
97622
97682
97708
97718
97721
97733
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97731

Fig. A3e-f

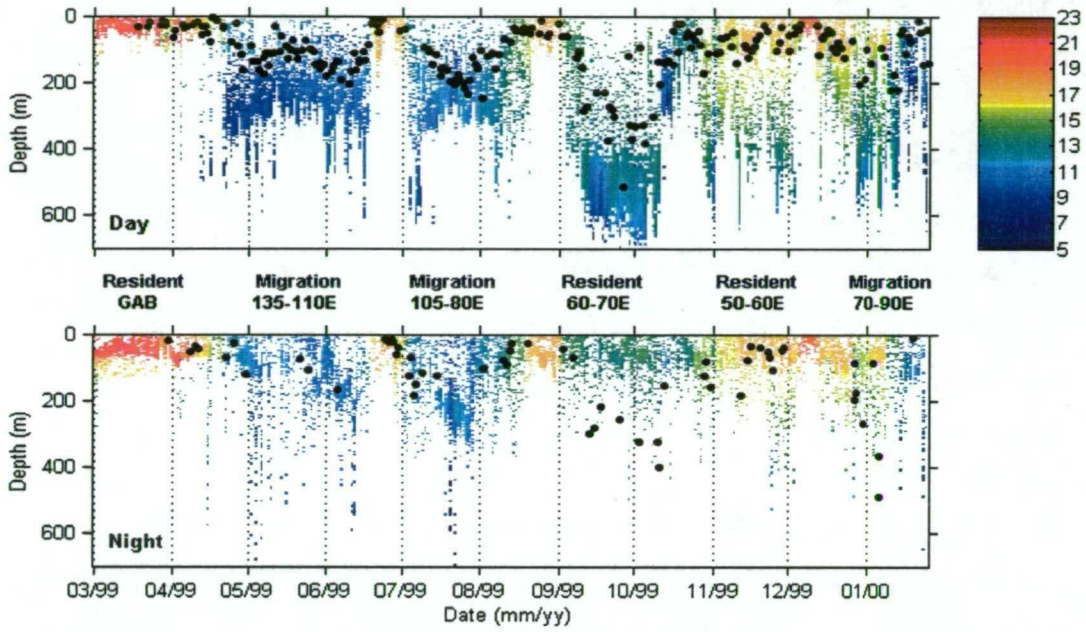


Fig. A3. Estimated daily intake (grams) per fish shows little variation either between regions or between periods of residency and migration; however foraging strategy and feeding depth vary markedly, indicative of significant switching between prey types during an annual cycle at sea. **a-d** Estimated daily intake (grams) per fish: **a,** GAB resident; **b,** Tasman Sea resident; **c,** Indian Ocean (IO) resident; **d,** Migration. The dashed horizontal line indicates global mean intake (grams). **e-f** Diurnal diving and feeding behaviour of one individual (SBT98-553, red track Fig. A2b) over an 11 month period (March 1999 – February 2000) at sea. Size at release: 111 cm LCF. Tag-based data recorded during **e,** day and **f,** night. Colour scale indicates water temperature (°C) at depth and black circles indicate a feeding event. Although the light sensor failed in late January 2000, the continuing temperature at depth data (not shown) indicates the fish re-entered the GAB in late February and remained resident there until April. The fish was subsequently recaptured the following summer in the GAB on 18 February 2001.

These new data provide insight into how the physiological capabilities of SBT support their extraordinary migrations. A key question remaining is why SBT undertake such lengthy migrations. Or rather, why do fish return to the GAB each year? Previous studies have indicated that while in the GAB juvenile SBT in fact experience their fastest growth, gaining 60% of their annual growth increment (Eveson *et al.* 2003). This may indicate that metabolic costs may be lower in the GAB, and/or that feeds in the GAB might have higher energetic content. Very hot calm days are common during summer in the GAB and SBT are known to 'sun bake' by spending lengthy periods in the shallowest few meters of the water column during the middle of the day. The archival tag data show this behaviour results in elevated body temperature (Gunn & Block 2001) which may result in lower metabolic cost and higher efficiency in the conversion of food to growth.

Once fish left the GAB, they traversed several major oceanic systems in the southern oceans with dramatically different vertical structures (Fig. A3e-f), and experienced ambient water temperatures between 3.5 and 25.7°C. This thermal niche for juvenile (20-30 kg) SBT is comparable with the 2.8 to 30.6°C range reported for adult giant Atlantic bluefin (100-400 kg) (Block *et al.* 2001). Throughout a migration circuit the time of day when feeding occurred and the depth ranges targeted both altered markedly (Fig. A3e-f). The diversity of SBT prey items has been observed to be much greater in oceanic waters as compared with shelf waters (Young *et al.* 1997), and the plasticity in diving and feeding behaviour documented here is consistent with the hypothesis that juvenile SBT are switching prey types through the course of their annual migration. We suggest that juvenile SBT have evolved as a wide-ranging, generalist predator in order to capitalize on the spatial and temporal heterogeneity of the temperate ocean.

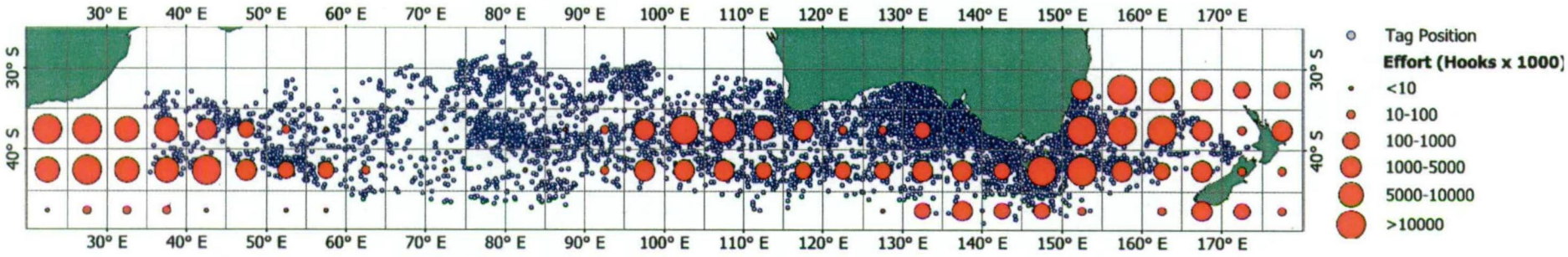
FISHERIES IMPLICATIONS

Catch rates from longline fisheries underlie stock assessments for all the tuna and billfish species. These were the sole data source used to derive the conclusion that industrial longline fisheries rapidly depleted the abundance of oceanic tuna and billfish resources by 90% in a recent meta-analysis that has received substantial

media attention (Myers & Worm 2003). For SBT, Japanese longline catch rates form the primary index of abundance used in the assessments. The large scale annual migrations and habitat use patterns revealed by these SBT archival tags, when compared to the distribution of longline catches and effort, highlights a critical shortcoming in the simple use of such data to estimate abundance trends – *i.e.* the failure to account for movements, spatial distributions and how these may change over time.

Catch rates can only provide information on abundance in the areas and time periods where fishing actually occurs, while fishing effort tends to be highly spatially concentrated and variable over time. However, implicit in almost all assessments reliant on catch rate is the assumption that the average density in areas without effort is equal to that with effort. As revealed by these archival tag data, SBT clearly spend substantial time in areas in which there is no fishing effort (Fig. A4). Changes in the relative density inside and outsides areas fished, particularly in combination with the contraction in the areas and time periods that have occurred in the Japanese SBT longline fishery, can induce substantial biases in catch rates as measure of abundance (Hilborn & Walters 1992). In addition, the archival tag data indicate that fish migrate through major concentration of longline effort during periods when the fishery is very active. In such situations, catch rates will reflect the rate of movement of animals through an area as well as localized density and can further confound interpretation of trends in catch rate. Finally, the variability in feeding and diving behaviour seen in the archival tags indicates that the effectiveness of a unit of fishing effort will vary in space and time. Simply treating all effort as equivalent under such circumstances will distort abundance trends from uncorrected effort data. Overall, the annual migration cycles and habitat use patterns revealed by these electronic tags present a significant challenge to the conventional standardization and uses of catch rates as measure of abundance. Caution is warranted in drawing conclusions about population changes simply based on trends in nominal catch rates.

a.



b.

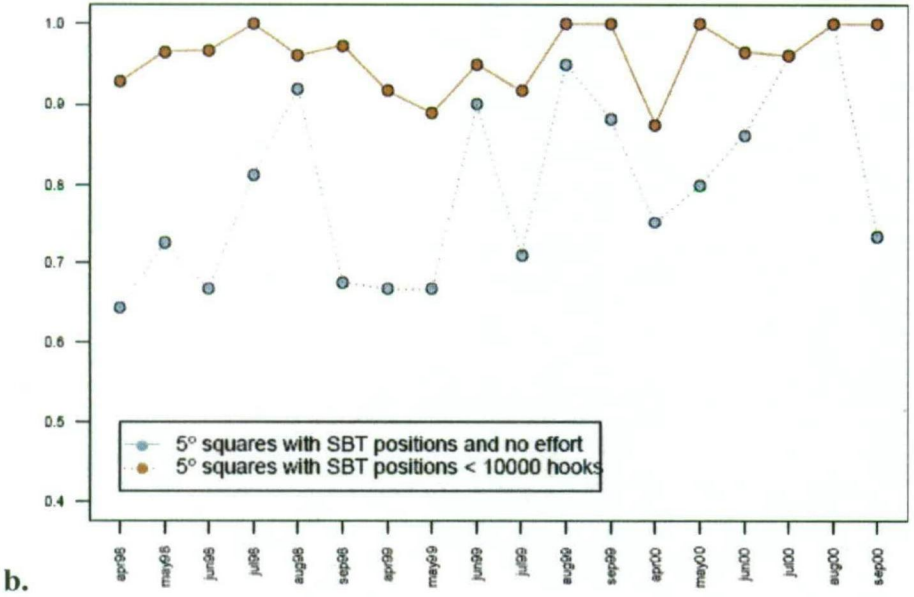


Fig. A4. Distribution of southern bluefin tuna as represented by positions obtained from juveniles (n = 30) implanted with archival tags in comparison with the distribution of fishing effort reported by the Japanese longline fleet. **a,** Black dots (n = 7952) represent locations estimated using light-based geolocation and sea surface temperature. Blue circles represent Japanese longline effort (number of hooks) by five-degree squares, as reported to the CCSBT, totalled across 1993-2001. Only squares contributing to the catch-per-unit-effort (CPUE) time-series used in the analytical stock assessments (statistical areas 4-9, months 4-9)(Basson *et al.* 2004) are included. **b,** Proportion of squares per month containing tag-based positions but no fishing effort.

Appendix A

METHODS

Tagging methods

An electronic tagging program was initiated in 1993 with six major releases of implantable archival tags in the Great Australian Bight between 1993 and 2000 as described previously (Gunn *et al.* 1994; Gunn & Block 2001). Briefly, all SBT were caught by pole-and-line using barb-less hooks and the tags surgically implanted into the peritoneal cavity ventral to the stomach. The SBT targeted were 2-4 year olds with caudal fork lengths ranging between 75 and 120 cm (mean size at release 95.98 ± 7.76 cm LCF). Fish were tagged with either Zelcon Technic P/L SBT100 (n = 88), SBT150 (n = 99), SBT200 (n = 138), or Wildlife Computers Mk7 (n = 200) archival tags. All tags types have a pressure sensor, photodiode light sensor and two thermistors: one thermistor external to the body to record water temperature; as well as an internal thermistor to collect data on visceral temperature (Gunn *et al.* 2001) (the latter excepting the Zelcon SBT100 tags). The Zelcon tags were programmed to record data from each sensor every four minutes for the first three months at liberty. Thereafter, these tags recorded for two consecutive days each week and then turned off for the remaining five days allowing data to be collected over a full year. The Wildlife Computers tags were programmed to sample every four minutes until the memory was filled (estimated to be five years after release).

A reward of $AUD250 was offered for tag return, and to date, 124 (24%) tagged tuna have been reported as recaptured by commercial operations, of which all tags but one have been returned. Of these, 95 have been successfully downloaded and processed using either the CSIRO software package ARCHTAG (Zelcon tags) or the Wildlife Computers proprietary software HexDecode v2.02 and Geocontrol v2.01 (Mk7 tags). Only short-term data from within the GAB was available from 39 tags due to early recapture by Australian purse-seine operations (n = 12), or early tag (n = 21) or light sensor (n = 6) failure. As the current study is primarily interested in determining migratory behaviours of juvenile SBT, the data from the remaining 56 tags only are included in this analysis.

Appendix A

Position estimation

Daily longitudes (n = 11361) were determined using light-based geolocation relating the mid-point between sunrise and sunset to Greenwich Mean Time (Hill 1994). Latitude estimates (n = 7952) were derived for the Mk7 tags by comparing the surface water temperature recorded by the archival tag with satellite estimates (Domeier *et al.* 2005). We used the freely available NOAA Multi-Channel Sea Surface Temperature (MCSST) global weekly 18km resolution level-3 product (night passes only). A 2 degree longitude strip centred on the geolocation longitude was searched from 20 to 60S, and shown here are the median positions of all MCSST pixels matching within ±0.2°C of the median tag SST recorded in the surface 5m during each 24-hour period. Using this method the latitudinal range, containing 90% of all pixel matches, was ≤3.87° for 95% of all positions estimated. The accuracy of the light- and SST-based geolocation estimates was validated as far as possible by comparing the reported release and recapture locations with the nearest available position estimate (usually ± 2 days). The root-mean-square errors in the light-based longitude were 0.66° (n = 30) and 1.14° (n = 13) compared with the release and recapture locations respectively; for SST-based latitude these were 0.51° (n = 30) and 1.04° (n = 7) respectively. All movement rates reported in the text only include data obtained with the Mk7 tags (*i.e.*, 1998-2000 releases). East-west movement is calculated based on a constant latitude of 37°S, being the median of all latitude estimates during non-GAB residency periods (*i.e.*, during April-December).

Feeding analysis

Bluefin tuna elevate their gut temperature as they digest food (Stevens & McLeese 1984). In SBT there is a very close relationship between the time to the maximum heat increment (T_{max}) and total intake of food in grams(Gunn *et al.* 2001). Incidence of feeding was calculated from visceral temperature records for each of the tuna whose tracks are shown in Fig. A2, and an estimate of food intake was calculated for each feeding event using the relationship T_{max} = 0.5845 × Intake calculated from the data in Gunn et al (2001). From this we calculated the average number of feeds per day and the mean intake amount. All results in this

study are reported as means ± s.d. Length to weight conversions were calculated using the formula $W = 3.131\ L^{2.9058}\ 1 \times 10^{-5}$ for SBT < 130cm LCF (Caton 1991).

ACKNOWLEDGEMENTS

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